STUDIES ON THE POLLEN OF NEW ZEALAND GYMNOSPERMS

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CORRIGENDA

P. 10 line 15: For 'Microcachyrdites' read 'Microcachryidites'.

P. 12 line 3: For 'Terasme' read 'Terasmae'.

P. 20 line 11: For 'sacci' read 'saccus'.

P. 31 line 19: For '3.3.3' read '3.2.3'.

P. 91 line 4: For 'delicately and evenly pitted' read 'scabrate to papillate'.

P. 92 Facing caption: For g. read 'Polar view; scabrate - papillate sculpturing'.

P. 93 lines 8 and 9: For 'pitted' read 'scabrate to papillate'.

P.162 line 3: For 'Brown' read 'Browne'.

P.176 In 7.8: For 'REPRESENTIVITIES' read 'REPRESENTATIVITIES'.

P.190 line 14: For 'fluctuate' read 'fluctuated'.

P.206 line 12: For 'representivity' read 'representativity'.

ADDITION TO FIGURE 36.

Pollen Percentages for *Dracophyllum*:

SAMPLE	
MOAST - 1	+
MOAST - 2	+
MOAST - 3	+
MOAST - 4	2
MOAST - 5	+
NTHST	+
MOAST - 6	
KIWIFT	
FANGST	
WILBFN	
KR 1	
KR 2	+
MKB-B	+
MKB-T	+
MOUNT RAKEAHUA	
TABLE HILL	+
AH-CB	+
AH-FH	3
AH-SW1	5
AH-SW2	2
AH-SW3	10
OMAN S1	+
OMAN S2	+

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ABSTRACT

This thesis has been particularly concerned with the interpretation of gymnosperm pollen percentages in modern and fossil pollen spectra in New Zealand. The morphology of the pollen of the indigenous gymnosperms was first studied to enable a correct identification of those types present in a sample to be made.

Dacrydium pollen can be identified specifically except for *D. bidwillii* and *D. biforme* which are inseparable; *Podocarpus* pollen is readily separated into groups but further identification, especially within the *P. totara* complex, is difficult; the three species of *Phyllocladus* possess small pollen grains making specific identification impossible, especially with the light microscope; and *Libocedrus plumosa* and *L. bidwillii* are similar in all characters and thus inseparable.

A new term, region of 'weakness', has been introduced for a feature previously not recognised in gymnosperm pollen. This region is adjacent to the dorsal roots of the bladders at the lateral margins of the cap and may have a function in harmomegathy.

Modern pollen rain has been studied quantitatively in South Westland where pollen percentages in moss cushions were compared to a quantitative assessment of the local vegetation surrounding the sampling sites; qualitatively at various localities in the South Island and Stewart Island; and qualitatively and quantitatively at Lady Lake, North Westland, where surface lake sediments and moss cushions

were analysed for their pollen content. Representation of pollen in surface samples is shown to be related to the pollination mechanism of each species present, the size of the plant and the structure of the local vegetation. Gymnosperm pollen is usually well represented because all species are anemophilous and thus produce large quantities of pollen. Most are trees (except *Dacrydium laxifolium* and *Podocarpus nivalis*) and their pollen is therefore released into the atmosphere above the vegetation from where it is effectively dispersed.

The Aranuian vegetation at Lady Lake was studied and for the last 5700 radiocarbon years has been broadly similar to that of the present day. The pollen analysis provides evidence for complexity in the development of Aranuian vegetation in Westland and also suggests that, locally, fluctuations in lake level have been responsible for subtle changes in the vegetation.

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CHAPTER 1

INTRODUCTION

A study of Quaternary vegetation is enhanced by a knowledge of the components of modern vegetation communities and their accompanying pollen rains. Comparisons of fossil assemblages of pollen grains to modern analogues from surface samples have been successful on the world context but in New Zealand work of this kind is still in its infancy.

Gymnosperms have dominated past floras of New Zealand and still form an important component of present day vegetation. They include six genera and twenty species, and a knowledge of the interplay of them with each other and with other plants in the pollen rain should provide a platform from which to make palaeoecological interpretations.

This thesis reviews past work over and above that which is specifically relevant to the other sections. The data presented in this review (Chapter 2) may not necessarily be directly comparable in sensitivity and precision to the data presented in the remaining chapters and this should be compensated for in the final summation.

The pollen morphology of the New Zealand gymnosperms was first described by Cranwell in 1940. Her work was based on light microscope observations and she found considerable difficulty in making specific identifications. This thesis revises the work of Cranwell using modern techniques of transmission and scanning electron microscopy correlated

with light microscopy. The information gained from this morphological study is then used in a survey of pollen rain from modern vegetation at various South Island localities in which gymnosperm species are dominant or codominant with other plant groups. After pollen analysis of a sample questions are frequently raised and relate to the significance of a certain percentage of one species when compared to another; the origin of the pollen, whether it is derived locally or from long distance transport; and the representation of a pollen type in relation to its representation in the vegetation. It is hoped that the results obtained from surface sample analyses reported in this thesis will provide the answers to such questions. The final application of the pollen morphological and pollen rain investigations is in the description of post-glacial (Aranuian) vegetation from pollen analysis of peat at Lady Lake in North Westland.

CHAPTER 2

LITERATURE REVIEW

2.1 POLLEN MORPHOLOGY AND IDENTIFICATION

Wodehouse (1935) provides an introduction to the pollen grains of gymnosperms and this has been further enhanced by the works of Erdtman (1943, 1957, 1965). The only detailed information available on the morphology of the pollen grains of the New Zealand gymnosperms is provided by Cranwell (1940). She demonstrates that the New Zealand species fall naturally into seven groups. Subsequent work by Cranwell (1942) and Couper (1953) give identification keys for the Podocarpaceae. From these it is clear that the specific identification of a single grain (with the exception of *Dacrycarpus dacrydioides* and *Dacrydium cupressinum*) is difficult unless the grain is favourably displayed to show the characters on which the key is based. The problem areas are: the *Podocarpus totara* complex encompassing *P. totara*, *P. nivalis*, *P. hallii* and *P. acutifolius*, and the *Dacrydium kirkii*, *D. biforme*, *D. bidwillii* group. It seems that if there are enough characters on which a description is based then any one grain orientation in a preparation would permit specific identification. Hansen and Cushing (1973) use eight qualitative characters and three dimensions to distinguish between the pollen of five species of *Pinus* in late Quaternary sediments from the Chuska Mountains, New Mexico. *Pinus* is known for the overall similarity of the pollen of

most of its members.

Other references to New Zealand material appear in Cookson (1947), Cookson and Pike (1953, 1954), Couper (1960), Thorburn (1974), Ueno (1960, 1974a,b) and Sivak (1975).

The previously quoted works have been carried out using the light microscope. Recent studies of gymnosperm pollen with the scanning electron microscope (e.g. Martin and Drew 1969; Adams and Morton 1972a; Hanover 1973; Ho and Sziklai 1973; Sivak and Carotini 1973; Ueno 1974a; Bagnell 1975; Planderova 1976) indicate its value in providing information for keys to the identification of pollen grains. This is shown in the elucidation of the minute and complex surface patterns not easily observed in light optical systems. The application of the scanning electron microscope in palaeobotany has been stressed by Taylor and Millay (1969), and while it may not replace the light microscope as the preferred instrument for making fossil pollen counts in palaeoecological studies it promises to advance our ability to identify pollen grains and spores (Martin 1969).

Little work has been published on the frequency of aberrant grains in the Podocarpaceae. Abnormal pollen grains have been described in other gymnosperm families, notably the Pinaceae, Cupressaceae, Taxodiaceae, Ephedraceae and Gnetaceae (Vishnu-Mittre 1957). Cranwell (1940) reports on abnormalities in the pollen grains of the New Zealand gymnosperms and suggests that these may be explained by a high incidence of hybridisation. Aberration in *Dacrycarpus dacrydioides* and *Acmopyle* (Cranwell 1961) is also recorded. The frequency varies from species to species and among

plants; the most common forms are those caused by variation in size and number of bladders.

2.2 THE ROLE OF STATISTICAL ANALYSIS IN IDENTIFICATION

A statistical approach to the determination of pollen has been employed by many workers. In particular, Cain (1940), Cain and Cain (1944), Christensen (1946), Buell (1946), Aytug (1960), Whitehead (1964), Ting (1966) and Mack (1971) have done this for *Pinus*, Harris (1956) for *Nothofagus*, and Martin (1959) for *Podocarpus*. Ting (1966) reports success with the method in which three measurements were used (*viz.* breadth of corpus, breadth of saccus and overall breadth) but Whitehead (1964) and Mack (1971) indicate that the reliability of the method is of a low order. It is worth considering the comments of Faegri and Iversen (1975):

> "On the whole the variability of pollen grains (and spores) should not be underrated. Both with regard to size and to morphological details pollen grains from the same species may exhibit great variations, and may transgrade into the sphere of variation of pollen of related species."

A good example of variability within a species is provided by Harris (1957) with *Nothofagus*.

Preparation techniques have been shown to alter the size and shape of angiospermous pollen grains (Christensen 1946; Praglowski 1970; Hanks and Fairbrother 1970). Less is known about the effects of these on gymnospermous pollen but Federova (1951, in Whitehead 1964) suggests that there is a comparable situation. However, others (Cain 1944; Whitehead 1964) have illustrated that no size difference results from three basic preparation techniques (potassium

hydroxide; acetolysis; potassium hydroxide and acetolysis) with *Abies* or *Pinus* pollen.

The mounting media also have characteristics which are undesirable for size frequency work. In glycerine jelly both fossil and modern pollen grains are known to swell over a period of time but there is no constant effect as some preparations exhibit essentially no size change (Whitehead 1964). Pollen mounted in silicone oil (Anderson 1960) of low viscosity tends to remain more spheroidal than in fluid media of high viscosity or solid media (Praglowski 1970). All pollen grains described in this study have been measured in both glycerine jelly, and in silicone oil of 2000 centistokes viscosity.

For a statistical approach to fossil pollen grain identification it must be taken into account that chemical changes take place during preservation and sedimentation, thus fossil grains may bear little resemblance to their modern counterparts.

Taking all the factors discussed in section 2.2 into consideration it seems reasonable to propose that identifications based on size are best viewed with some reserve.

2.3 THE DEVELOPMENT OF THE GYMNOSPERM POLLEN GRAIN

The identification of pollen and spores is based on the size, shape and ornamentation patterns of the outer wall (exine). The pollen wall nevertheless is of considerable interest and may hold some clues to the specific identification of pollen grains. In most vascular plants the pollen wall consists of two fundamentally different layers: an inner, more or less cellulosic layer (intine)

which is usually destroyed upon acetolysis; and an outer, acetolysis resistant layer (the exine) which is composed of oxidative polymers of carotenoids and/or carotenoid esters known as sporopollenin (Walker and Doyle 1975). The exine is further subdivided into the outer sexine layer and the inner nexine layer. The two-layered exine in most gymnosperms investigated consists of an inner laminated layer (or nexine) and an outer one consisting of orbicules as in *Libocedrus*, and/or a sculptured granular-alveolate layer (or sexine) as in *Podocarpus* (Gullvåg 1966; Walker 1976).

Elaborate pollen sculpturing seems correlated with entomophily, while psilate pollen grains are largely characteristic of anemophilous plants (Whitehead 1969). The fact that gymnosperm pollen is generally not highly sculptured is then perhaps related to their anemophily. More than one type of alveolate pollen is recognised in the gymnosperms. In advanced gymnosperms, particularly in the pollen of the Pinaceae (van Campo and Sivak 1972) exine sections have an irregular spongy appearance, while in pollen of the Cycadaceae the exine seems to have a quite different more organised honey-comb like appearance (Skvarla and Rowley 1970). Most significantly, some gymnosperms have a granular type of exine (van Campo and Lugardon 1973) which is considered to have led to the alveolate exine in gymnosperms and columellate pollen of the angiosperms (Walker 1976).

The ontogeny of the gymnospermous pollen wall has attracted comparatively little attention, only *Pinus banksiana* (Dickinson 1971, 1976; Dickinson and Bell 1972, 1976), *Pinus contorta* (Ho and Sziklai 1971; Ho and Owens 1974), *Pinus*

sylvestris (Willemse 1971), *Pinus balfouriana* (Ting and Tseng 1965), *Pseudotsuga menziesii* (Owens and Molder 1971) and *Podocarpus macrophyllus* (Vasil and Aldrich 1970) having been studied in any detail. Significantly, the sexine forms the basis for all identification and thus the foundation for the science of pollen analysis. A summary of the formation of the sexine as described by Dickinson (1976) in *Pinus banksiana* follows: immediately following tetrad formation large vesicles are generated in the cytoplasm by membranous cisternae not unlike enlarged dictyosomes. These accumulate at the periphery of the spore cytoplasm subjacent to the plasma membrane through microtubule organisation, make contact and finally the outer face of the vesicles fuse with the plasma membrane. Simultaneously, the outer and radial faces of the vesicles join to form a continuous membranous layer. Further cytoplasmic activity now takes place with the generation, by dictyosomes, of small vesicles which move to the membrane and fuse with it. These vesicles add height to the developing sexine by secondary deposition of carbohydrate and growth of initials. At this point the vesicular remains (i.e. sexine initials) are acetolysis resistant. After displacement of the plasma membrane by sexine the dictyosomes become less frequent and the structures associated with nexine formation arise in the cytoplasm. Following formation of several layers of nexine the grains are released from the tetrad and float freely in the thecal fluid. Both sexine and nexine are now resistant to acetolysis. Rapidly the sexine initials become massively thickened and following this little change takes place prior to the release of the grain from the microsporangium.

There are numerous reports of a lamellar inner part of the exine of pollen grains (Gullvåg 1966; Rowley and Southworth 1967; Dickinson and Heslop-Harrison 1968; Sengupta and Rowley 1974; Rowley and Dahl 1977). When discussing the fine structure of gymnosperm pollen walls these workers suggest that a laminated nexine results when the unit membranes which presumably excrete the sporopollenin run parallel to the plasma membrane. In *Podocarpus macrophyllus* (Vasil and Aldrich 1970) the formation of sexine and nexine is definitely related to deposition of sporopollenin on "tapes" or lamellae of unit membrane dimension. The intine is a homogenous layer and does not show any lamellation or fibrous character.

Most members of the Podocarpaceae family possess bladders (Wodehouse 1935). They are generally regarded as organs of flight (Procter and Yeo 1973) and unquestionably give the pollen grains greater dispersal, aiding in fertilisation. Where bladders are found they are always associated with the furrow. When the grain dries they close over the furrow forming a protection for it (i.e. harmomegathic response) and it seems reasonable to suppose that the survival of the furrow was made possible by the presence of the bladders.

The bladders are regarded as being formed by a distension of the sexine of the pollen wall (Afzelius 1956; Ueno 1958; Gullvåg 1966; Dickinson and Bell 1970). Such distension results from the expansion of material giving a clear periodic acid - Schiff's reaction inserted between the sexine and nexine layers at the tetrad stage of development (Dickinson and Bell 1970). The sexine bounding the

expanding bladder is plastic and displays staining properties different from mature sporopollenin indicating the presence of a hemicellulose matrix. Dickinson and Bell propose, however, that the bladders represent comparatively minor modifications of normal exine structure because the sexine of the corpus increases in thickness simultaneously with the expansion of the bladders.

2.4 GYMNOSPERMS IN THE FOSSIL RECORD OF NEW ZEALAND

There have been numerous works published in the last 30 years which provide a summary of the known occurrence of gymnosperm pollen in the fossil record; especially significant are the works of Cranwell (1938) and Couper (1953, 1960). Many fossil types are recognised which bear similarity to pollen grains of the present day gymnosperms, but some (e.g. *Microcachrydites antarcticus*) have no modern counterparts.

Pollen of the Podocarpaceae is abundant in the New Zealand fossil record (Couper 1951). They first appeared in the lower Cretaceous and remained until the upper Eocene when the flora began to assume its modern aspect (Harris 1953). *Podocarpus (Dacrycarpus) dacrydioides* type enters the record in the lower Oligocene; *Podocarpus* cf. *spicatus* in the Pliocene; *Podocarpus* cf. *ferrugineus* and *Podocarpus* sp. (*totara-acutifolius* group) in the upper Miocene (Couper 1953, 1960). The pollen of *Dacrydium cupressinum* first appears in the lower Oligocene. A closely related type (*D. prae-cupressinoides*) has been recognised in lower Cretaceous beds, perhaps suggesting a longer history for *D. cupressinum*. *Dacrydium* sp. (*kirkii-bidwillii* group) is first recorded in the Miocene.

Macko (1957) records pollen of the New Zealand species *Dacrydium cupressinum*, *Podocarpus nivalis* and *P. spicatus* in the Miocene of Poland. *Phyllocladus* has a long history, and pollen similar to that of the living species is present in deposits from the upper Eocene (Couper 1960). The fossil genus *Phyllocladidites* Cookson ex Couper is very abundant in the lower Cretaceous.

Araucarian pollen occurs sparingly from the Jurassic onwards - notably the Ohai coals of the upper Eocene - where pollen similar to that of *Agathis australis* is found (Couper 1951). Due to the similarity of the pollen of all species of this family it has been recorded as *Araucariacites* cf. *australis* Cookson (Couper 1953).

Libocedrus appears in the Pliocene but as Couper (1951) remarks, its pollen is very delicate and easily destroyed and probably has a much longer history in New Zealand.

2.5 MODERN POLLEN ANALYSIS

Pollen analysis of peat, lake sediments, marine sediments and alluvial deposits provides information which is relevant to the reconstruction and understanding of past flora and vegetation. The interpretation of the data is complex (Birks 1970) and requires a thorough knowledge of the present day ecology of the flora involved and also information on the relationships between modern pollen rain and the vegetation from which it is derived. Judicious use of surface samples from a variety of vegetational regions and formations may be expected to add considerably to our understanding of the pollen rain-vegetation relationship.

Numerous studies have concentrated on this

relationship either by analysing lake surface sediments, and/or moss cushions, or by using variously designed pollen traps (e.g. King and Kapp 1963; Terasme and Mott 1964; Tauber 1967; R.B. Davis 1967; Davis 1968; McAndrews and Wright 1969; Whitehead and Tan 1969; Davis, Brubaker and Beiswenger 1971; Davis and Brubaker 1973; Crowder and Cuddy 1973; Janssen 1973; Rymer 1973; Singh, Chopra and Singh 1973; Ritchie 1974; Dodson 1977; Hicks 1977). Further studies (e.g. Davis and Deevey 1964; M.B. Davis 1967a,b; Davis, Brubaker and Webb 1973; Pennington 1973; Hicks 1974; Bonny 1976; Craig 1978) have utilised traps to gauge pollen influx and obtain absolute pollen frequencies. According to Davis, Brubaker and Webb (1973) this may be interpreted as a census of trees and so reaffirm the potentiality of pollen analysis as a precise instrument for studying the history of vegetation. Hicks (1974) outlines a method whereby modern pollen rain values can be used not only to interpret pollen diagrams in terms of vegetational history but also to provide an absolute time scale for such changes. The potential of the method is considerable as long as the modern and fossil samples are derived from the same region.

Recently, sophisticated numerical analyses have been applied to modern pollen spectra. O'Sullivan and Riley (1974), Birks, Webb and Berti (1975), Ritchie and Yarranton (1978) and Caseldine and Gordon (1978) have used multivariate techniques for data analysis to show that modern, qualitatively defined, vegetation-landform types can be characterised by means of contemporary pollen spectra. Cluster analysis reveals a similar pattern (Birks 1973) thus justifying the use of fossil pollen spectra as a means of

reconstructing the relative composition of past vegetation on such scales. Nevertheless, despite this numerical justification it is necessary to have a knowledge of the nature of pollen dispersal and pollen production before a balanced interpretation can be placed on modern pollen rain data. Problems arise at the margins between two vegetation types when one type produces little pollen in relation to the other. The tundra-forest margin in North American vegetation is one such example (Davis 1969).

In numerical analysis of Quaternary material, Harris, Darwin and Newman (1976) have demonstrated, using discriminant function and association analyses, the existence of groups of types whose associations persist over the whole of New Zealand. These are then applied in forming climatic interpretations from pollen analytical data. Harris *et al.* (1976) propose that the methods employed are logical extensions of those based on percentage sums, dominant types and indicator assemblages. The latter has been discussed by Harris and Norris (1972) for the New Zealand Quaternary.

The proportion of pollen types found in a sample do not reflect the real composition of the vegetation because the relative abundance of pollen types is determined by pollen production and dispersal (Janssen 1966, 1970, 1973). Tauber (1965, 1967, 1977) recognises three components of pollen dispersal in a forest area *viz:* trunk space which he considers the most important; pollen transported above the canopy; and pollen carried to higher altitudes by convection currents and then deposited by rain-out. The extent to which the vegetation of an area is represented in a pollen

diagram depends on the share of each of the three components in the total pollen deposition. Indices of pollen dispersal have been coined by Hamilton (1972) and Flenley (1973) who classify pollen types on their relative dispersal power and relative export respectively. The physical attributes of the forest must therefore be considered in any assessment of pollen dispersion.

Raynor, Hayes and Ogden (1974) have shown that the forest modifies pollen dispersion primarily by changing the local meteorological conditions and flow patterns and secondarily by direct removal of particles. The greater influence of any one of the above factors or components to the total exclusion of the others will result in over-representation which, as Janssen (1973) points out, is frequently observed and will always be much debated. Janssen has suggested that pollen analysis of sediment cores from lakes which, except for submerged aquatics, do not have a pollen producing vegetation is often preferred for the reconstruction of vegetational history from pollen diagrams.

Pollen production and pollination mechanism are of similar importance when considering modern pollen spectra. Entomophilous species generally produce a smaller quantity of pollen than anemophilous plants and consequently are less likely to appear in modern pollen spectra. Similarly, trees growing in the upper canopy produce more pollen than shrubs growing in the understorey of a forest and are therefore more likely to be favourably represented in surface samples collected outside the forest. The height and strength (Janssen 1973) and exposure of the pollen source affects the dispersal distance. Faegri and Iversen (1964) provide some

notes on the relative pollen production of certain species, and Faegri and van der Pijl (1966) give an outline of pollination mechanisms and their relationships to pollen dispersal.

2.6 POLLEN ANALYSIS OF MOSS CUSHIONS

According to Faegri and Iversen (1964, p. 35): "as both the rate of growth of the moss and that of destruction of pollen grains are unknown, the method has its obvious shortcomings, but may be used with some caution." Pollen extracted from moss cushions is taken as representing the past few years. Carroll (1943) and Benninghoff (1960) suggest an age span of 5-15 years. Hicks (1977) is more cautious stating that the exact number of years is indeterminable but still considered long enough to be free of wild yearly fluctuations. Ritchie (1974) has demonstrated that moss cushion samples show as much variability within as between vegetation regions because of local effects. Local community composition is indicated and regional pollen rain is variably masked.

Pollen destruction is an important consideration in the final analysis of moss cushion samples. Crowder and Cuddy (1973) observed corroded exines of *Carya* and *Ulmus*. Subsequent experimental work by Frederickson (1978) with *Ginkgo* and cycad pollen demonstrated that in nature pollen which remains unburied for several months will undergo natural oxidation and thus become more susceptible to destruction by bacteria and alkaline ground water. This may well apply to the microenvironment of a moss cushion.

2.7 MODERN POLLEN RAIN STUDIES IN NEW ZEALAND

Studies of the modern pollen rain from New Zealand vegetation are at an early stage of investigation despite the pioneer work of Filmer and Harris (1949). Clark (1951) and Licitis (1953) conducted atmospheric surveys in cities to discover what pollen and spores were in the air at any one time as a guide to the diagnosis and possible cures of asthmatic complaints. These workers laid out glass slides, coated with glycerine jelly, which were mounted on an exposure device equipped with a wind vane to keep the slide vertical and facing into the wind. Their results illustrated that exotic tree pollen (*Pinus*, *Quercus*, *Cupressus*, *Betula*, *Salix* and *Platanus*) and the indigenous pollen types Gramineae, *Nothofagus* and the conifers were the most abundant atmospheric components. Wind transportation of pollen was thus the most notable feature borne out by the surveys, especially that of *Nothofagus* which was distributed far beyond the actual distribution of the trees (Licitis 1953). Such long distance transportation is also noted by Moar (1969a) where analysis of a surface sample from Antipodes Island revealed pollen of indigenous conifers, *Pinus*, *Nothofagus fusca* type,* *Metrosideros*, *Plantago* and Chenopodiaceae presumably originating in mainland New Zealand. Surface samples analysed from the Chatham Islands (Dodson 1976) record pollen of *Podocarpus*, *N. fusca* type and *Phyllocladus* while drillholes in Quaternary peat also on The Chathams (Mildenhall 1976) record these types as well

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* *Nothofagus fusca* type includes *N. fusca*, *N. truncata*, *N. solandri* var. *solandri* and *N. solandri* var. *cliffortioides*.

as *Dacrydium cupressinum*, *Dacrydium biforme/bidwillii* type and *Ascarina*. Similar results have been obtained by Moar (1958) in Auckland Islands peats. Moar (1969b) reported the possibility of long distance transport of pollen of the genus *Casuarina* to New Zealand undoubtedly derived from Australia. Many recently published pollen diagrams (e.g. McGlone and Topping 1977) also note this pollen type and since there is no record of it ever growing in New Zealand in recent times, provide support for the early assumption of long distance transportation. Close *et al.* (1978) discuss aerial dispersal of biological material from Australia to New Zealand and provide a summary of numerous other observations of trans-Tasman dispersal and the westerly drift of pollen grains and fern spores.

Mainland pollen rain studies have compared the pollen spectra to vegetation near the sampling station, and the results achieved are of considerable value in interpreting post-glacial pollen sequences. Moar (1970) made the first advances in our knowledge of pollen dispersal from native vegetation types in New Zealand. These results emphasised that there is a difference in pollen dispersal between wind and insect-pollinated plants and that uplifted pollen from lower altitudes will effectively mask the open treeless character of local alpine vegetation whose components are largely insect-pollinated. Forest samples were very much influenced by the pollen of the dominant tree at the sampling site and consequently the complexity of the forest was not always adequately indicated by the pollen spectra. Generally wind pollinated plants were well represented by comparison to insect-pollinated plants, except on the

Travers Range, Nelson, where shrubby conifers were scarcely recorded despite their covering considerable areas.

McKellar (1973) and Myers (1973) employed Tauber designed pollen traps to estimate the representation of *Nothofagus* pollen in surface spectra as its presence in post-glacial pollen diagrams is difficult to interpret with clarity. Myers confirmed the work of Licitis (1953) that *Nothofagus* is an important element of the pollen rain up to 60 km (mostly west) from source areas while McKellar concluded that *N. fusca* type is disseminated far greater distances and in greater numbers than is the pollen of *N. menziesii*.

CHAPTER 3

MATERIALS AND METHODS

3.1 NOMENCLATURE

Allan (1961) classified the New Zealand gymnosperms into three families of five genera and twenty species. De Laubenfels (1969) has since separated *Podocarpus dacrydioides* from the genus *Podocarpus* because of its many unique features including the possession of a three bladdered pollen grain, and this now becomes *Dacrycarpus dacrydioides*. Recent work by Wardle (1972) has recognised a new variety (*Podocarpus totara* var. *waihoensis*) derived by introgressive hybridisation between *P. totara* and *P. acutifolius*. Apart from these two nomenclatural changes the classification of Allan (1961) is followed throughout. In addition, Philipson (1965) and Moore and Edgar (1970) are consulted when species lists are compiled for pollen rain sampling sites.

3.2 POLLEN MORPHOLOGY

3.2.1 Terminology

The terms employed in the morphological descriptions are based primarily on Kremp (1965) and Heusser (1971) with the addition of terms used by Wodehouse (1935), Cranwell (1940), Erdtman (1957, 1965), Yamazaki and Takeoka (1959), Kapp (1969) and Ho and Sziklai (1973). Walker (1976) was consulted when describing the sectioned exine. These terms

are defined below. Figure 1 illustrates particular structural features and schematically represents the various sculpturing and reticulum types encountered in the Podocarpaceae.

alveolate - irregular spongy appearance of the sexine layer.

apolar - lacking symmetry or with the proximal and distal poles undifferentiated.

bilateral - only two vertical planes of symmetry.

bisaccate - possessing two sacci (bladders).

bladder - membranous appendage in vesiculate pollen grains (synonymous with sacci, wing).

cap (cappa) - the proximal portion of the corpus or body.

"cauliflower type" protrusions - irregular protrusions on the cap of the pollen grain.

chagrenate - translucent, individual structure particles are not recognisable.

columella - a columnlike or rodlike structure that interconnects the nexine with the sexine.

corpus - the body or central part of vesiculate pollen.

distal pole - that part of a spore or pollen grain that faces to the outside when a member of a tetrad.

exine - the outermost resistant layer of the pollen wall.

furrow - a longitudinal area functioning as the germinal pore, differing from the remainder of the surface generally in the unadorned and thinner character of the sexine.

furrow rim - the lip of the furrow, the edge or fold of exine bounding the furrow, sometimes thickened in vesiculate grains, bearing the ventral roots of the bladders.

granular - composed of elements <1 μm in size and radially more or less isodiametric.

harmomegathy - volume-change accommodation.

heteropolar - with proximal and distal portions dissimilar as to shape, apertures, and sculpture.

infratectal - confined to the space between the nexine and the overlying sexine.

intine - the inner, slightly resistant layer of a pollen or spore wall. At the germination of the pollen the intine protrudes, forming the membrane of the pollen tube.

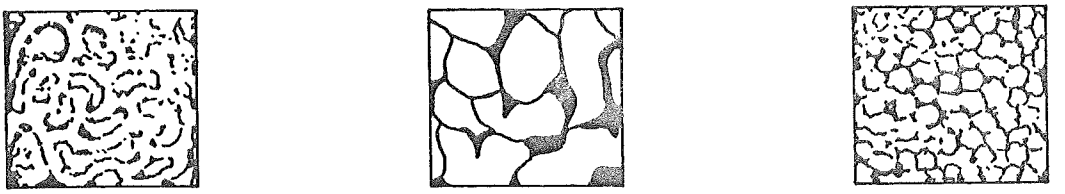
Figure 1. Schematic representation of structural features, cap sculpture and bladder reticulum types in pollen of the Podocarpaceae.

A. Cap sculpture:
   a. chagrenate-rugulate;
   b. rugulate;
   c. tuberculate.

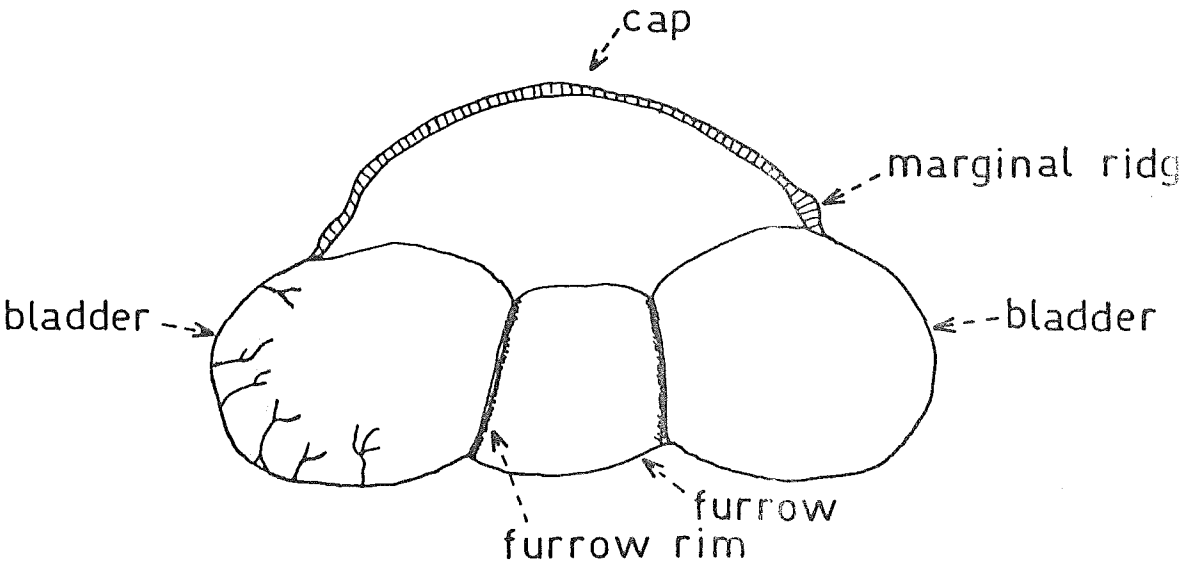
B. Diagrammatic lateral longitudinal optical section.

C. Bladder reticulum structure:
   a. indistinct reticulum, large meshed with heavy relief lines (muri);
   b. distinct but delicate reticulum with more-or-less equal, regularly distributed, elongated and polygonal meshes;
   c. distinct reticulum with unequal irregularly distributed, elongated meshes of various sizes and outlines;
   d. distinct reticulum with heavy relief lines and elongated meshes near the ventral roots but become smaller meshed towards the periphery;
   e. indistinct reticulum with infrequent meshes and heavy relief lines which run in a line from the point of attachment of the bladder to its periphery;
   f. distinct reticulum, irregularly large meshed with heavy relief lines;
   g. distinct reticulum, small meshed forming thickened polygons with heavy relief lines;
   h. distinct reticulum, large meshed forming a blindly branched system with heavy relief lines.

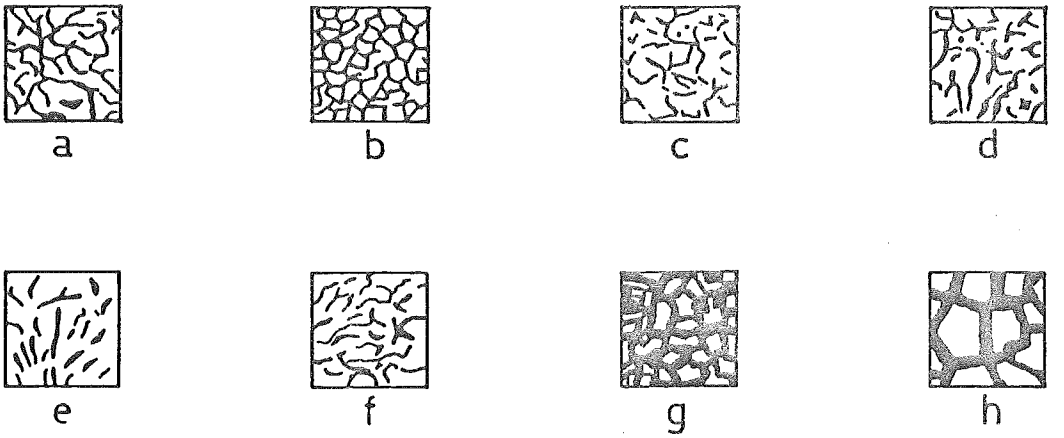
A Types of cap sculpture:



B



C Types of bladder reticulum structure:



lateral longitudinal - synonymous with equatorial, with special reference to the view seen at right angles to the polar axis.

marginal ridge - the slightly projecting rim of the cap.

meshes - network of thickenings comprising the reticulum of the bladder.

micropunctae - perforations in the outer wall of the bladder.

monad - a pollen grain occurring singly, as opposed to pollen in tetrads or polyads.

muri - the ridges bordering the meshes in a reticulum.

nexine - the inner, non-sculptured part of the exine.

orbicule - star-shaped components of the sexine in *Libocedrus* pollen.

papilla - roundish, protuberant area of the exine provided for the exit of the pollen tube.

pitted - marked with small depressions.

proximal pole - the side facing inward in the tetrad.

pseudopore - differs from a true pore in that it is not the normal exitus place of the pollen tube.

reticulum - a netlike sculpture in which the meshes are of greater dimension than the intervening ridges or muri.

rugulate - a sculpture of elongate and irregular elements (rugulae).

sculpture(ing) - ornamentation, or the external appearance of the sexine.

sexine - the sculptured part of the exine.

spinose - spiny, having spines.

spinule - small spine not exceeding about 3 µm.

tectate-imperforate - the nexine is completely veiled by the sexine.

tectate-perforate - nexine not completely veiled by the sexine and frequently exposed.

trisaccate - possessing three sacci (bladders).

tuberculate - knobby protrusions on the sexine surface.

vesiculate - possessing bladders.

white-line lamellations (tapes) - lamellar membranes in the nexine layer.

3.2.2 Source of Material

Pollen collections were made from living specimens, which flowered between 1975 and 1978,* and from existing herbarium specimens at the Department of Botany, University of Canterbury (CANU), and Botany Division, D.S.I.R., Lincoln (CHR). As many as four specimens of each species were collected and examined, and data relating to each sample is presented in tabular form in Chapter 4. Examinations were made with the light, scanning and transmission electron microscopes.

3.2.3 Preparation of Pollen

The male cones were boiled in water until softened (usually 5 minutes) and then macerated through a 100 µm mesh sieve. The material was then flushed into a centrifuge tube with distilled water, centrifuged and decanted. The procedure continued as follows (after Erdtman 1960; Faegri and Iversen 1964):

i. successive washes with 30% and 100% glacial acetic acid;

ii. acetolysis with freshly prepared Erdtman's acetolysis fluid (9 parts acetic anhydride: 1 part concentrated sulphuric acid). This was heated slowly over a period of 3-5 minutes until boiling, centrifuged and decanted.

iii. i. repeated but in the reverse order;

iv. washed in distilled water (twice);

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*Voucher specimens of many of these are deposited in the herbarium, Department of Botany, University of Canterbury.

v. some of the residue was mounted in a safranin-glycerine mixture;

vi. the remaining residue was dehydrated through a series consisting of 95% ethanol, absolute ethanol (twice), 50% ethanol: 50% tertiary-butanol, tertiary-butanol (twice);

vii. mounted in silicone oil (AK 2000 centistokes -cst) (Anderson 1960).

3.2.4 Size Measurement and Photography

Measurements were made in both silicone oil and glycerine jelly; this is in contrast to Couper (1953) whose measurements were made directly in neither mounting media. Since all pollen analytical work is based on preparations in either media measurements made in such media would therefore be more directly applicable. Because pollen grains swell in glycerine jelly it is generally accepted that their measurements need to be divided by 1.25 to make them relative to measurements made in silicone oil mounts. For the Podocarpaceae (i.e. winged gymnosperms) four dimensions were taken but for *Libocedrus* and *Agathis* (i.e. non-winged gymnosperms) only their diameter was measured. Measurements were made using a Reichert Zetopan microscope equipped with a calibrated eyepiece micrometer. Measurements made on members of the Podocarpaceae were (refer Figure 2):

a. overall length of the grain in the expanded condition (a-a'),

b. the shortest diameter of the corpus (b-b'),

c. the bladder length (c-c'),

d. the furrow width (d-d') coinciding with the bladder edges.

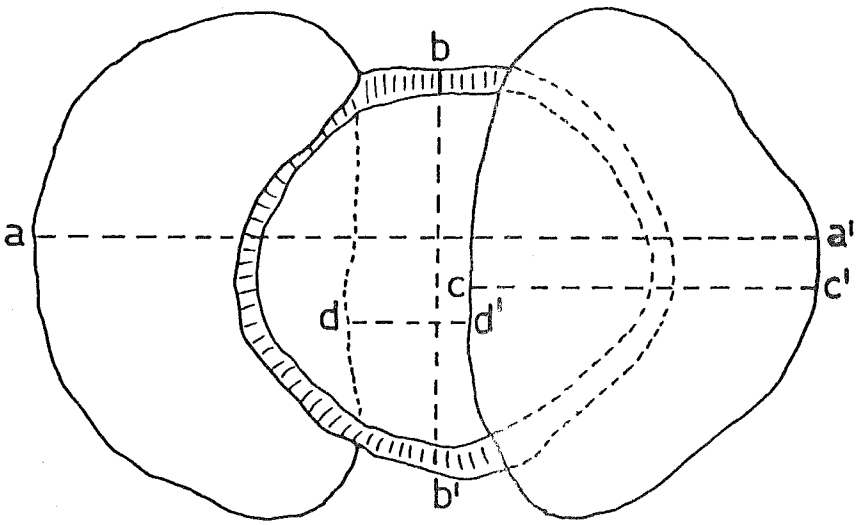

Figure 2. Measurements made on the pollen grains of the Podocarpaceae.

These are quoted in Chapter 4 (Tables 2, 4 and 6) as a range with mean and standard error.

Thirty pollen grains from each species prepared in both mounting media were used for size statistic measurements. Cranwell (1940) suggested that size statistics may be operative in distinguishing *Dacrydium bidwillii* from *D. biforme*, and *Podocarpus spicatus* from *P. ferrugineus*. In these instances a sample size of 30 was employed for two specimens of each species but only the overall length was measured. Pollen grains from two specimens of each species were examined.

Photographs were taken of pollen mounted in glycerine jelly in a Leitz Ultraphot microscope using Pan F film.

3.2.5 Scanning Electron Microscopy

The method used for pollen preparation for scanning electron microscope observations is that described by Adams and Morton (1972b). It involves acetolysing the pollen sample (as described in 3.2.3) and then dehydrating it through an ethanol series of 25%, 50%, 90% and 100% (twice). Amyl acetate, which probably removes any residual oils or waxes remaining after acetolysis and dehydration, was added and the sample filtered through filter paper (Whatman No. 1). The filter paper containing the pollen was then transferred to a carbon dioxide bomb for critical point drying. After drying, the desiccated pollen was mounted on a specimen stub using "microstik" and coated with 1 µm of gold in a Polaron SEM Coating Unit E5000. The specimens were examined and photographed, either with a Cambridge Stereoscan 600

scanning electron microscope operating at 15 or 25 Kv equipped with a Nikon F2 35mm camera loaded with Ilford FP-4 film, or with a JEOL JSM-35 scanning microscope equipped with a Mamiya 120mm camera loaded with Ilford 120 film.

3.2.6 Transmission Electron Microscopy

Sporangia were excised from male cones, either from fresh material, or from herbarium specimens, plunged into 3% glutaldehyde in 0.025M phosphate buffer (pH 7.3) and fixed for 6-10 hours (or overnight) at room temperature (*ca.* 20°C). After washing the sporangia were placed in 2% osmium tetraoxide for 4 hours in the same buffer. The material was then dehyrdrated in ethyl alcohol through 25%, 50%, 75%, 95% and 100% stages, transferred to propylene oxide and embedded in Araldite and left to polymerise for 48 hours at 40°C and 24 hours at 60°C. Thin sections were cut on an LKB Ultrotome II, stained in potassium permanganate and examined in an Hitachi HS-7S electron microscope and photographed using Agfa Scientia plates developed in microphen.

3.2.7 Germination of *Libocedrus* pollen

In pollen germination experiments the following method was employed: Fresh pollen, collected from plants growing in the Christchurch Botanic Gardens, was placed on 0.5% agar on microscope slides. To the agar 10% lactose had been added and the pH was adjusted to 5.5 (based on Stanley and Linskens 1974, p. 68; Ho and Rouse 1970). The slides were inverted, placed above moist filter paper in petri dishes and incubated at 25°C. When pollen had germinated (usually after 2-3 days) the material was

examined under a Leitz Ultraphot microscope and photographed.

3.3 POLLEN ANALYSIS

3.3.1 Modern Pollen Analysis - Locality and Site Selection

To assist the interpretation of fossil pollen assemblages extant vegetation types were sampled for modern pollen rain. Since little was known of the pollen representation of many of the New Zealand gymnosperms it was decided to sample forests in which they were the predominant components. National Forest Survey Type maps (Masters, Holloway and McKelvey 1957) were obtained from Mr G.P. Allan of the New Zealand Forest Service, Westland Conservancy, and from these appropriate vegetation types in the Harihari district, South Westland, were located, and subsequently sampled. This was done in the period July 1976 to February 1977. The general locality of this region and all other surface sampling sites discussed in this thesis are indicated on Figure 3. In mid-1977 another modern pollen rain study was initiated at Lady Lake, North Westland, during the course of a survey of potential macrofossils by Miss Hilary Drake (Masterate Student, Department of Botany, University of Canterbury). The samples obtained from Ajax Hill, South-east Otago, were collected by Mr Matt McGlone in 1975. The analysis of these sites gave inconclusive information on the role of *Phyllocladus*, *Dacrydium biforme* and *Libocedrus bidwillii* in the modern pollen rain. Further samples were therefore collected from the Wilberforce River Valley, Canterbury, and Kelly Range, Westland, where these

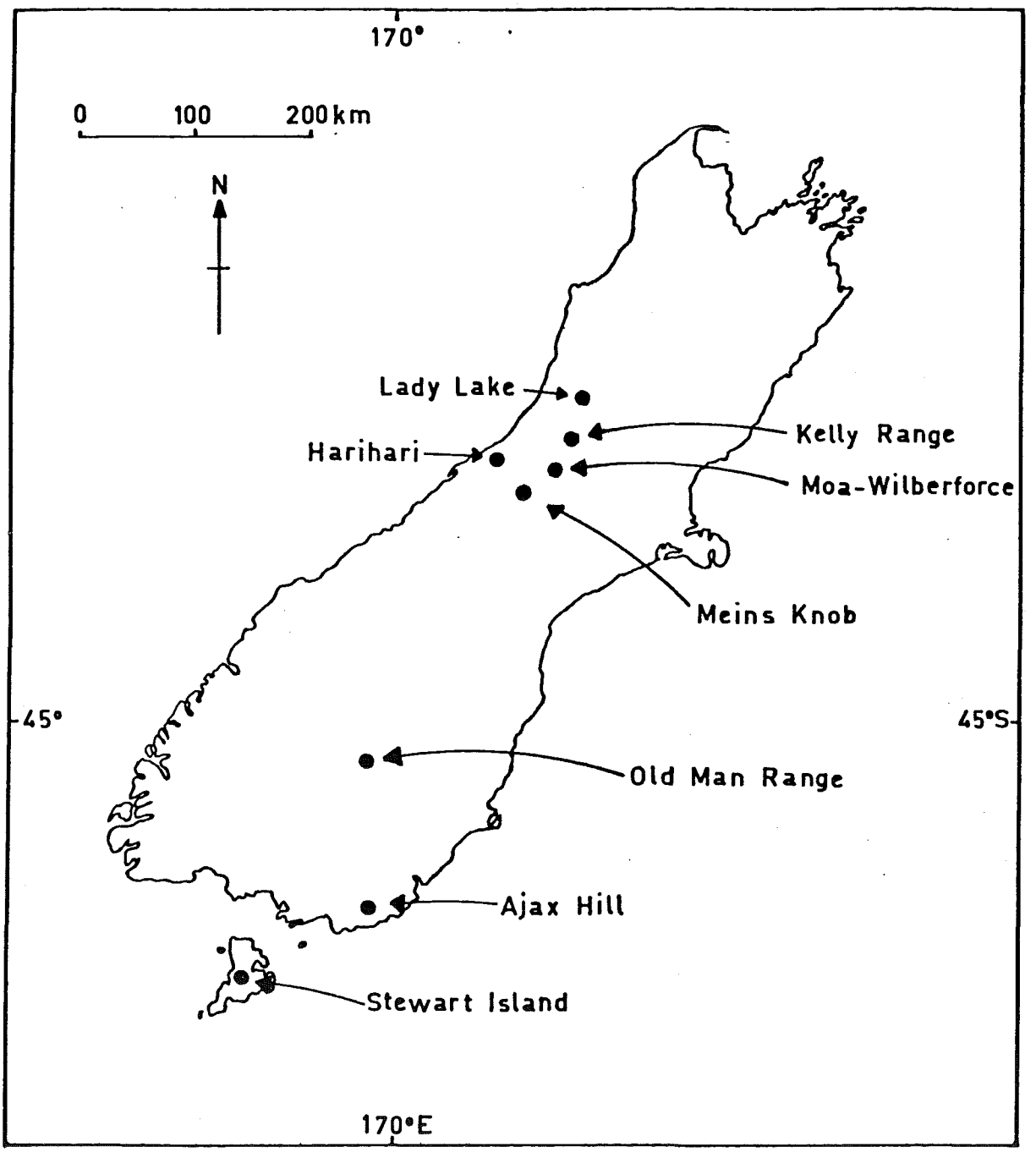

Figure 3. The general locality of all surface sampling sites discussed in Chapters 5, 6 and 7.

three species are relatively abundant in the vegetation. These samples were collected in the summer of 1977-78 and the sites for them were first located on aerial photographs. Surface sample analysis from Stewart Island; Old Man Range, Otago; and Meins Knob, Canterbury, were facilitated through the collections of Dr Colin Webb, Mr Matt McGlone and Dr Colin Burrows, respectively.

For each sample site a detailed locality map is provided, compiled from New Zealand Department of Lands and Survey NZMS series published in the period 1968-1971.

3.3.2 Methods of Modern Pollen Rain Sampling

Moss and liverwort cushions of similar thickness and texture were used to determine the pollen rain at each site. At Lady Lake surface sediment samples were also used. To minimise the possibility of differential filtration of pollen and spore types the whole thickness of the cushion was removed (Crowder and Cuddy 1973; Dodson 1976). To avoid over-representation of canopy species in forested areas the moss cushions were collected in openings of the forest. Where this was not possible they were collected under the canopy. Each moss cushion was a composite of 4-6 subsamples which were collected randomly throughout a square metre. At sites around Harihari a measure of the sampling variability was obtained by calculating the standard error of the mean.

Lake sediments were collected with a Peterson grab sampler, constructed by Mr Ian Johnson (Department of Botany, Workshop), and then transferred to small sampling bottles for transportation to the laboratory. A lake contour survey was carried out from a 3.5 m dinghy using a Ferrograph echo sounder.

Seven Tauber designed pollen traps constructed in the Geography Department, University of Canterbury, were set up at various locations in the Harihari study area to study the pollen rain from March 1976 to March 1978. Because of heavy rainfall, human interference and animal damage the programme proved unsuccessful and was abandoned.

In the laboratory the samples were prepared by standard chemical treatments (Erdtman 1960). They were firstly boiled in 5% sodium hydroxide, sieved, acetolysed (as described in 3.2.3) and where necessary pretreated with hydrofluoric acid before being mounted in silicone oil or glycerine jelly.

3.3.3 Vegetation History - Sampling and Radiocarbon Assay

The vegetation history of Lady Lake was studied from a core obtained from a narrow band of peat close to the road at the eastern margin of the lake. Samples were collected using a Hiller corer with a 50 cm chamber. Preparation of samples for pollen analysis followed that set out in 3.3.3; samples for radiocarbon assay were air-dried in the laboratory and then forwarded to Krueger Enterprises (Inc) Cambridge, Massachusetts (GX-4574) and to the New Zealand Radiocarbon Dating Laboratory, Geological Survey Lower Hutt (K32/f1,K32/f2). The radiocarbon age scale (in years B.P.*) has been corrected according to the bristlecone pine tree-ring chronology for the northern hemisphere (Fergusson 1968) for dates within the last 8000 years. The dates obtained in

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*Years before 1950.

this study fall within this time span and are quoted as corrected ages. The method of Damon, Long and Wallick (1972) was used to correct the date GX-4574.

3.3.4 Pollen Counting and Identification

Pollen and spore counts were carried out, using a Reichert Zetopan microscope, at a magnification of x 400 and not less than 200 pollen grains were counted per sample along successive traverses of the slides. In the light of principles discussed by Brookes and Thomas (1967), on the distribution of pollen grains on microscope slides, it was decided to avoid counting those grains which were close to the edge of the coverslip. In some surface samples locally abundant types dominated the pollen spectrum so counting proceeded until at least 200 tree pollen types were recorded.

Pollen grain identification was aided by reference collections of slides held in the Departments of Geography and Botany at the University of Canterbury and was supplemented by slides of gymnosperm pollen prepared and described in Chapter 4 of this thesis. The published works of Cranwell (1940) on gymnosperms, Cranwell's (1942) pollen key, and McIntyre (1963) on the Myrtaceae, were also consulted in conjunction with an experimental key compiled by Mr Matt McGlone (unpublished). Unidentified pollen and spores appear under the title 'unidentified' in all pollen diagrams; they rarely amount to more than 3% of the pollen sums. The broad titles *Coprosma*, *Nothofagus fusca* type, Cyperaceae, Gramineae and Compositae adopted in this thesis, and most New Zealand studies, encompass many species often with varying ecological amplitudes and due to basic

uniformity in pollen morphology are extremely difficult for a pollen analyst to deal with.

Appendix I lists the pollen types and their nearest identification in the reference material of the Geography Department, University of Canterbury, collection.

3.3.5 Data Treatment and Presentation

Each pollen type was assigned a number and an abbreviated name of four characters. The counts for each type in each sample were transferred to standard 80 column data cards which were then run on two computer programmes (Dodson 1972). The first programme POLLIST, is a listing and checking programme. The data is tabulated so that under each abbreviated name, the data for every surface sample and/or core level is listed. This output appears in Appendix II. The second programme, PLNSPRS, is a multi-purpose programme but was used primarily to provide percentage calculations from any specified base sum. These results were then plotted on pollen diagrams of standard format.

The base sum on most occasions was the total pollen and spores counted. At some sampling sites (especially the Moa-Wilberforce region) it was necessary to exclude heavily over-represented local types from the sum. These are subsequently noted on the pollen diagrams. Where vegetation analysis data (basal area) is available it is compared to the pollen frequencies for the major tree and shrub taxa.

3.4 VEGETATION SAMPLING

3.4.1 Harihari, South Westland

Species abundance in the vegetation sampled in the Harihari district was determined during the summer of 1976-77. A quantitative study was made of the vegetation at each site as follows: A transect 5 m wide by 30 m long was marked off and all woody stems greater than 1 cm girth breast height (i.e. at 1.5 m above ground surface) were identified and measured. A minimum of 100 individuals were counted which often meant that the sample area had to be extended. The data were later converted to per cent basal area (≡ relative dominance).* Data for the major species are tabulated in Chapter 5 and that for the minor species, as well as species lists for each site, are presented in Appendix IIIa. The basal area measure takes some account of the higher pollen production of larger trees (Davis and Goodlett 1960) and despite difficulties in its use permits an interpretation of the relationships existing between vegetation and pollen rain to be made (Whitehead and Tan 1969).

The density of ground cover plants was also assessed. The number of plants (includes seedlings) were counted in successive 1 × 5 m quadrats spaced along the original transect. Counting ceased when the number of new species encountered was nil. These results were then converted to density per square metre and are listed in Appendix IIIa.

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*Calculated thus:

$$\text{basal area \%} = \frac{\text{basal area of species}}{\text{total basal area}} \times 100$$

3.4.2 Other Sampling Areas

Quantitative measurement of the vegetation at Lady Lake was carried out by Miss Hilary Drake and resulted in calculation of per cent basal area similar to that employed in the Harihari study area. For details of the "constant count" method used at Lady Lake refer to Drake (1977). Johnson, Mark and Bayliss (1977) carried out vegetation analyses at Ajax Hill. The results of these two surveys appear in Appendices IIIb and IIIc, respectively. Species lists for the sampling sites are recorded in the original works.

At all other stations the vegetation was visually appraised, and the field notes of numerous collectors have been used in providing vegetation descriptions at each individual sampling site. Much of the information regarding regional vegetation has been obtained from published works and is qualitative. More reliable interpretation could be placed on modern pollen rain work if vegetation data for much larger areas was available.

CHAPTER 4

POLLEN MORPHOLOGY OF THE NEW ZEALAND GYMNOSPERMS

4.1 INTRODUCTION

In this chapter the pollen morphology of the New Zealand gymnosperms is presented. Descriptive notation follows the format used by Heusser (1971). All pollen examined and the collection data relating to each sample are presented in Tables 1, 3 and 5. Tables 2, 4 and 6 summarise light microscopic measurements, corpus shape and cap sculpturing of all pollen. Following the descriptions a key to the identification of the New Zealand gymnosperm pollen is presented.

4.2 PODOCARPACEAE

4.2.1 *Dacrydium* Solander

Dacrydium is a genus of evergreen trees allied to *Podocarpus* and consisting of about 20 species, chiefly native of New Zealand, the Malay Peninsula, Indo-China, Thailand, New Guinea, Borneo, Australia, Tasmania, New Caledonia and Chile (Fitzpatrick 1929; Dallimore and Jackson 1966). There are seven species in New Zealand all of which are endemic.

The pollen morphology of the New Zealand *Dacrydium* was first studied in detail by Cranwell (1940). Her work showed that *Dacrydium cupressinum*, *D. bidwillii*, *D. biforme* and *D. kirkii* form one distinct group while *D. colensoi*,

Table 1. *Dacrydium* pollen examined, geographical location, collector and herbarium reference.

TAXON	LOCALITY	COLLECTOR	HERBARIUM REFERENCE
Dacrydium cupressinum	Atuanui State Forest, Northland	R.E. Beever	CHR[1] 256770
	Ruakura, Waikato	A.L. Poole	CHR 191000
	Lady Lake, Westland	D.T. Pocknall	CANU[2] 25252
Dacrydium bidwillii	Old Channel Bog, Manapouri, Fiordland	C.J. Burrows	CANU 12756
	Bealy Chasm, Arthurs Pass National Park	D.T. Pocknall	CANU 25260
	Bealy Chasm, Arthurs Pass National Park	G.H. Stewart	-
	Dew Lakes, North-east Nelson	J.R. Dodson	-
Dacrydium biforme	Adams Burn, Lake Te Anau, Fiordland	W.R. Philipson	CANU 47
	Kelly Range, Otira, Westland	D.T. Pocknall	CANU 25250
	Takapari Road, Ruahine Range, Manawatu	W. Simmons	CANU 25243
Dacrydium kirkii	Puketi State Forest, Northland	R.C. Lloyd	CANU 25246/48
Dacrydium colensoi	Gouland Downs, North-west Nelson	H. Talbot	CHR 152901
	Otari Gardens, Wellington	B.P. Molloy	GEOG[3] 176
	Wanganui State Forest, Westland	D.T. Pocknall	CANU 25254/55
Dacrydium laxifolium	Christchurch Botanic Gardens, Canterbury	B.P. Molloy	-
	Upper Otira River, Arthurs Pass National Park	C.J. Burrows	-
	Top of Otira Gorge, Arthurs Pass National Park	D.T. Pocknall	CANU 25258
	Big Bog, Saltwater State Forest, Westland	K.D. Smith	CANU 25256
	Karangarua State Forest, Westland	K.D. Smith	-
Dacrydium intermedium	Worsley Pass, Poulter River, Canterbury	C.J. Burrows	CANU 2097
	Deniston Scenic Reserve, South-west Nelson	D. and G.C. Kelly	CHR 25011
	Tabernacle Hut, Karamea, Westland	R. Mason	CHR 58078

[1] Botany Division, D.S.I.R. Herbarium

[2] Department of Botany, University of Canterbury Herbarium

[3] Geography Department, University of Canterbury (Slide reference)

Table 2. Summary of pollen measurements,[1] corpus shape and cap sculpturing[2] in *Daerydium*.

TAXON	TOTAL LENGTH		CORPUS BREADTH		BLADDER LENGTH		FURROW WIDTH		CORPUS SHAPE	DORSAL CAP SCULPTURE
	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE		
Daerydium cupressinum	48.16 ± 0.54 (42.5 - 51)	50.06 ± 0.67 (44.2 - 54.4)	34.3 ± 0.42 (30.6 - 37.4)	38.59 ± 0.50 (34 - 40.8)	19.81 ± 0.45 (15.3 - 23.8)	19.81 ± 0.38 (17 - 22.1)	8.32 ± 0.31 (6.8 - 10.2)	8.92 ± 0.32 (6.8 - 10.2)	Spheroidal	Coarsely tuberculate-rugulate
Daerydium bidwillii	53.17 ± 0.57 (47.6 - 57.8)	62.13 ± 0.73 (56.1 - 68)	28.20 ± 0.51 (25.5 - 34)	31.37 ± 0.57 (27.2 - 37.4)	19.16 ± 0.47 (17 - 23.8)	24.34 ± 0.41 (20.4 - 27.2)	14.53 ± 0.35 (11.9 - 17)	13.60 ± 0.48 (10.2 - 17)	Spheroidal to ellipsoidal	Tuberculate-rugulate
Daerydium biforme	55.59 ± 0.89 (51 - 64.6)	68.08 ± 0.85 (61.2 - 74.8)	33.74 ± 0.62 (27.2 - 37.4)	40.20 ± 0.68 (35.7 - 44.2)	21.25 ± 0.36 (18.7 - 23.8)	26.61 ± 0.36 (23.8 - 28.9)	12.24 ± 0.45 (10.2 - 17)	15.13 ± 0.35 (13.6 - 17)	Spheroidal to ellipsoidal	Small tuberculate-rugulate
Daerydium kirkii[3]	43.27 ± 0.93 (34 - 51)	53.55 ± 1.10 (44.2 - 61.2)	23.29 ± 0.59 (20.4 - 27.2)	30.71 ± 0.58 (25.5 - 34)	16.77 ± 0.50 (13.6 - 20.4)	20.99 ± 0.63 (17 - 25.5)	9.44 ± 0.50 (6.8 - 13.6)	11.73 ± 0.52 (6.8 - 15.3)	Ellipsoidal	Small tuberculate
Daerydium colensoi	50.93 ± 0.95 (51 - 68)	59.16 ± 0.97 (51 - 68)	33.75 ± 0.78 (27.2 - 42.5)	31.62 ± 0.66 (27.2 - 37.4)	22.57 ± 0.44 (20.4 - 27.2)	22.69 ± 0.55 (20.4 - 27.1)	15.30 ± 0.35 (13.6 - 17)	15.38 ± 0.36 (13.6 - 18.7)	Spheroidal to rhomboidal	Small tuberculate
Daerydium laxifolium	64.43 ± 0.83 (54.4 - 68)	73.64 ± 0.67 (68 - 81.6)	32.81 ± 0.50 (30.6 - 37.4)	36.72 ± 0.47 (34 - 40.8)	22.18 ± 0.47 (17 - 23.8)	26.95 ± 0.50 (23.8 - 30.6)	20.65 ± 0.50 (17 - 23.8)	22.27 ± 0.47 (17 - 25.5)	Ellipsoidal	Tuberculate
Daerydium intermedium	58.44 ± 0.85 (52.7 - 64.6)	67.10 ± 0.64 (61.2 - 71.4)	28.81 ± 0.48 (25.5 - 34)	31.28 ± 0.45 (27.2 - 34)	19.46 ± 0.26 (17 - 20.4)	22.78 ± 0.36 (20.4 - 27.2)	16.40 ± 0.31 (13.6 - 18.7)	19.55 ± 0.31 (17 - 22.1)	Spheroidal to ellipsoidal	Tuberculate-rugulate

[1] Mean with standard error followed by range in parenthesis. All measurements in microns (µm).

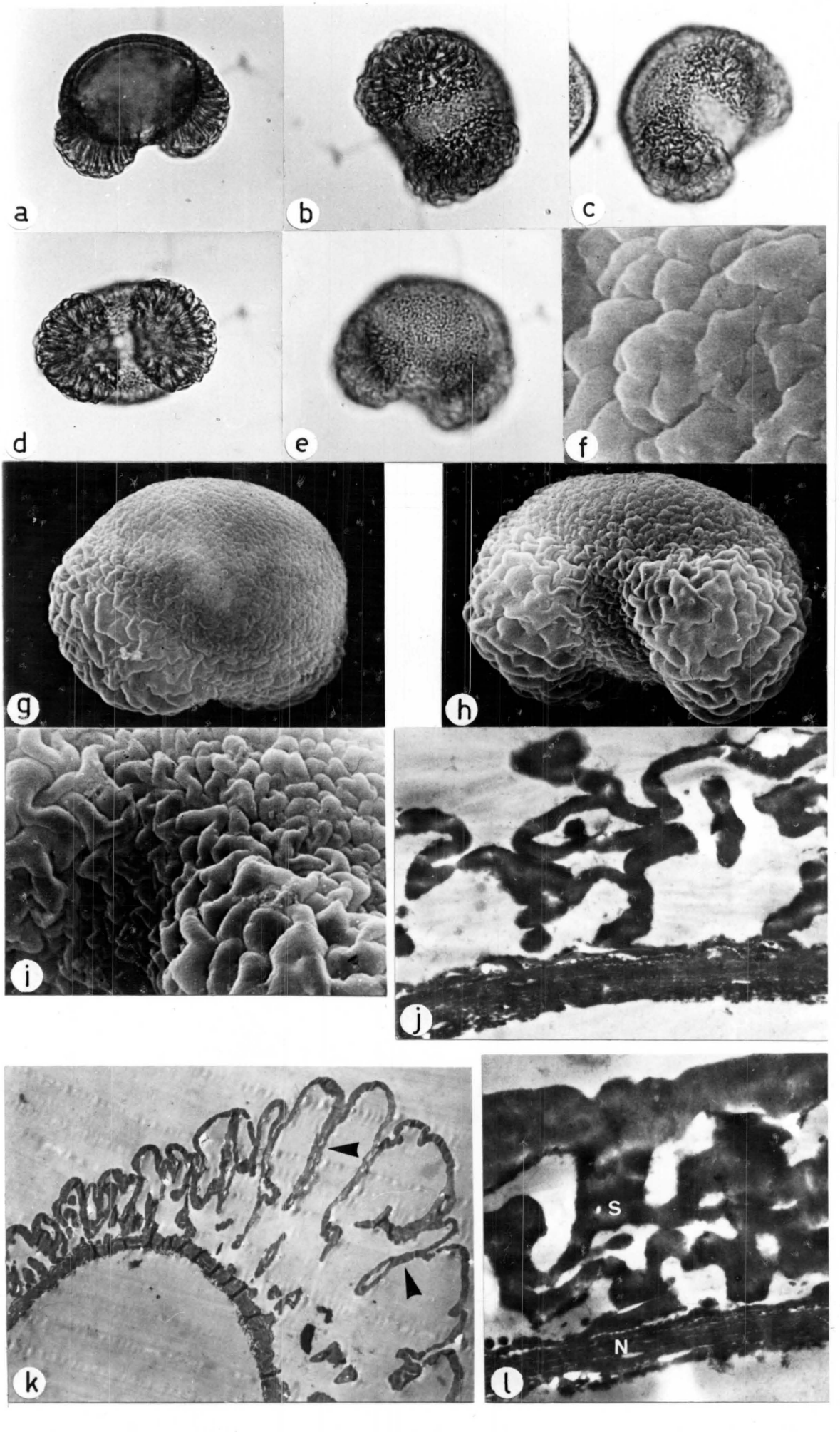
[2] Only predominant type quoted; other types are discussed in the text.

[3] Only one specimen of *D. kirkii* studied.

Figure 4. *Dacrydium cupressinum.*

a - e. Light micrographs (all x 900).
f - i. Scanning electron micrographs.
j - l. Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (distal); rugulate furrow sculpturing.
c. Polar view (distal); small bladders with radial thickenings.
d. Polar view (distal); small bladders with radial thickenings.
e,f. Dorso-lateral view; tuberculate-rugulate cap sculpturing (f x 8600).
g. Dorso-lateral view; small bladders and spheroidal cap (x 1650).
h,i. Lateral longitudinal view; coarse sculpturing over the entire grain (h x 1750, i x 4300).
j. Section through furrow; rugulate sculpturing (x 18000).
k. Section through bladder; infratectal sexinous elements (arrowed), rugulate cap sculpture at the point of attachment of the bladder to the cap (x 4700).
l. Section through tectate cap; large alveolate sexine (S), on a basement laminated nexine (N) (x 22000).


a
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D. intermedium and *D. laxifolium* are like the *Podocarpus* type because of the absence of radial internal thickenings of the bladders and the suggestion of a furrow rim. On the basis of this and subsequent work (Cranwell 1942), *D. cupressinum* was shown to be easily recognisable and more closely related to *D. gibbsiae* than to any of the pollen of the other species in the group. Both have puffed or rudimentary bladders and small furrows. Similar groupings within the genus have been described on the basis of wood anatomy (Patel 1967a; Pocknall 1977) although *D. colensoi* is clearly distinct.

The pollen of *Dacrydium* spp. occurs frequently in peat and one particular area of concern is the specific identification of *D. biforme* and *D. bidwillii*. These two species often appear similar in the field and their pollen and xylem are also similar morphologically. One of the aims of this work is to decide whether it is possible to confidently confirm the existence of either *D. biforme* or *D. bidwillii* in a pollen sequence.

Descriptions of Pollen

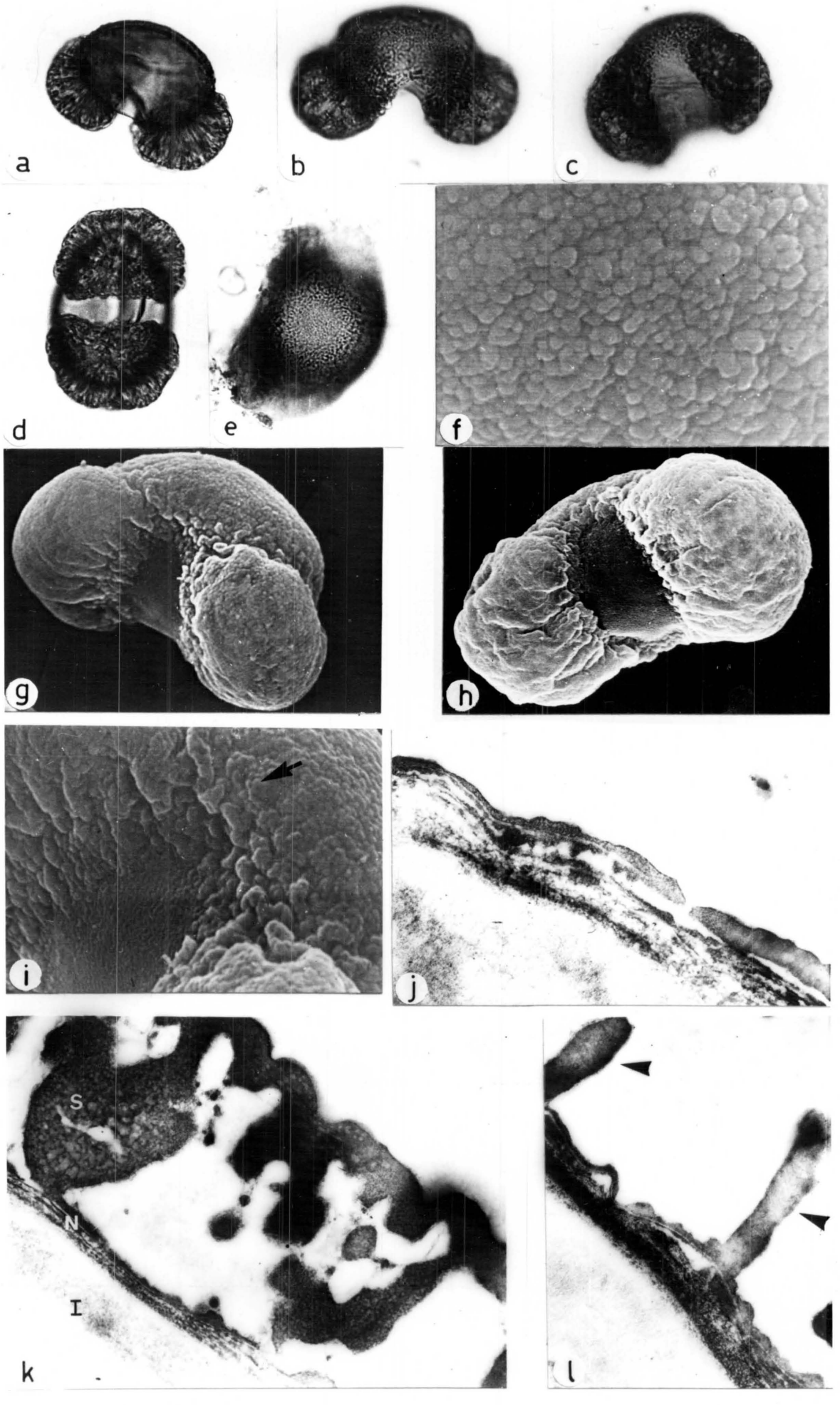
All grains are monads, heteropolar, bilateral; vesiculate and bisaccate unless otherwise stated.

Dacrydium cupressinum Solander (rimu) Figure 4a-l.
Cap spheroidal; coarsely tuberculate-rugulate (Figs 4e,i) over most of cap but inconspicuous rugulate marginal ridge at the dorsal roots of the bladder. Exine tectate-imperforate with large alveolate sexine and laminated basement nexine (Fig. 4 l). Bladders hemispherical in polar view (Fig. 4d); not protruding far beyond the corpus when

Figure 5. *Dacrydium bidwillii.*

a - e Light micrographs (all x 800).
f - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Lateral longitudinal view; radial thickenings in bladders.
b. Lateral longitudinal view.
c. Ventro-lateral view; sharp distinction between cap and furrow.
d. Polar view (distal); bladders irregular in outline.
e,f. Polar view (proximal); tuberculate cap sculpturing (f x 2900).
g. Lateral longitudinal view (x 1550).
h. Polar view (distal) (x 1550).
i. Lateral view; indistinct marginal ridge (arrowed) and rugulate furrow (x 4000).
j. Section through furrow (x 27000).
k. Section through tectate cap; sexine (S) thick and alveolate, nexine (N) and intine (I) (x 38000).
l. Section through nexine in bladder region; sexinous elements (arrowed) radiate from the nexine to the bladder margins (x 23000).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fully expanded; internally they consist of infratectal sexinous elements or bladder intrusions (Fig. 4k). Bladders and furrow intersect sharply (Fig. 4b), with no furrow rim; cap and furrow mostly continuous (Fig. 4h); furrow rugulate (Fig. 4j).

The few aberrant grains seen included three bladdered grains, thus possessing a triangular furrow, and those which had a bladder completely surrounding the corpus.

Cookson (1957, p. 47) comments: "the peripheral margin of the air sacs are composed of well defined peripheral loops of mesexinous thickenings giving a crenulate appearance." Transmission microscopy (Fig. 4k) reveals that the bladder consists of infratectal sexinous elements or bladder intrusions (based on Hess *et al.* 1973) which Ikuse *et al.* (1978) suggest are homologous with the columellae which can be seen in the exine of the proximal surface of the corpus.

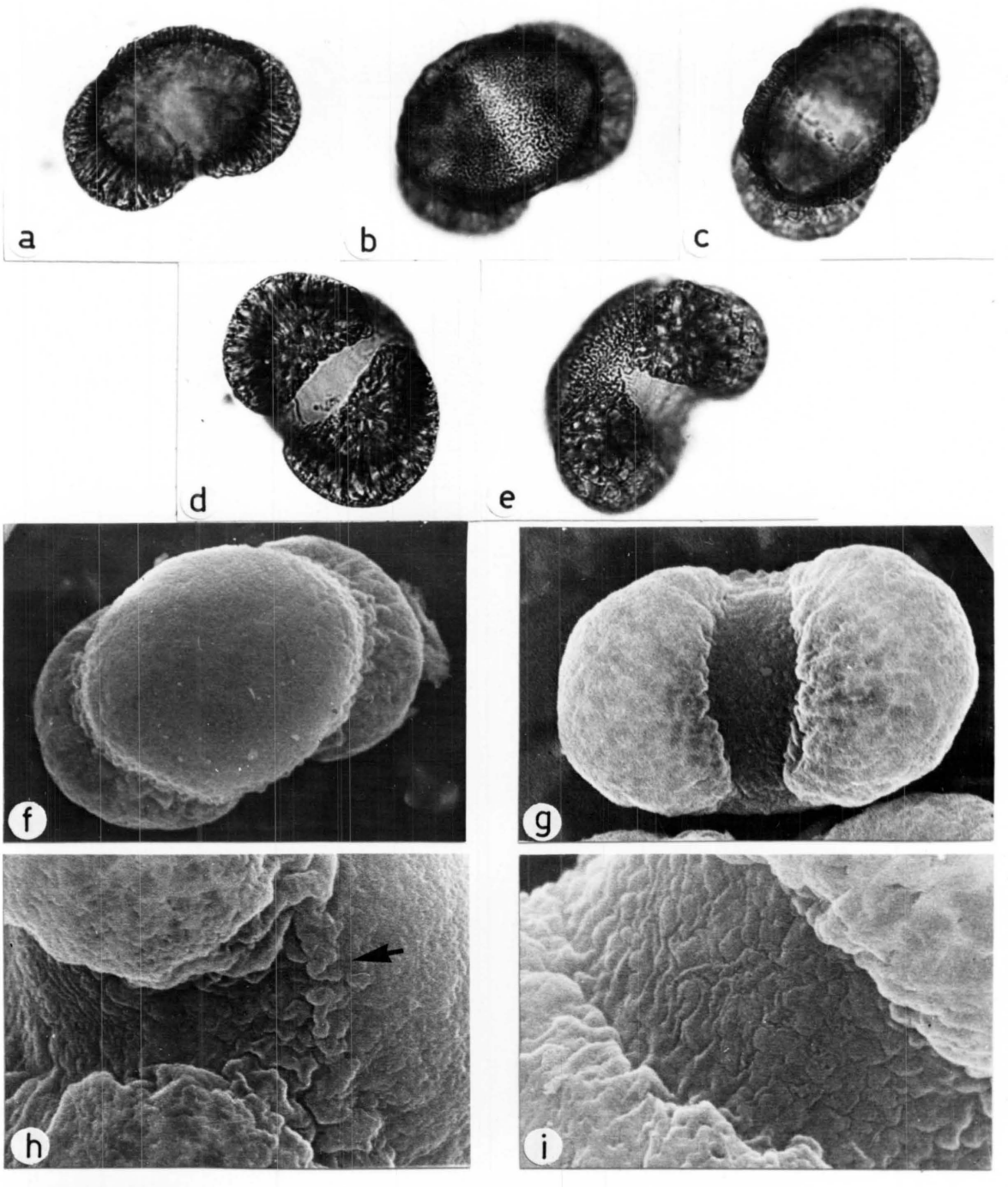
The pollen of *D. cupressinum* is easily recognisable even when badly distorted in peat preparations. In size it is comparable to only *D. kirkii* but they are not often confused because of differences in bladder structure and cap sculpture.

Dacrydium bidwillii Hook. f. ex Kirk (bog pine) Figure 5a-l. Cap spheroidal to ellipsoidal; tuberculate (Figs 5e,f) differentiating into a pronounced marginal ridge (Fig. 5i); sexine large alveolate, almost columellate (Fig. 5k). Bladders hemispherical (globose in lateral section);

Figure 6. *Dacrydium biforme*.

a - e Light micrographs (all x 800).
f - i Scanning electron micrographs.
j - k Transmission electron micrographs.

a. Lateral longitudinal view; thick exine.
b. Polar view (proximal); small tuberculate-rugulate cap sculpturing.
c. Polar view (proximal), ellipsoidal body and thick exine.
d. Polar view (distal); clearly defined bladders with radial thickenings.
e. Lateral longitudinal view; sharp distinction between cap and furrow.
f. Polar view (proximal) (x 1350).
g. Polar view (distal); hemispherical bladders (x 1350).
h. Lateral view; marginal ridge (arrowed) and cap sculpturing (x 3000).
i. Polar view (distal); rugulate furrow sculpturing (x 3400).
j. Section through tectate cap; sexine (S), nexine (N) and intine (I) (x 28000).
k. Section through furrow (x 31000).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turgid; sometimes irregular in outline (Fig. 5d) and occasionally united at their margins encircling the furrow; characterised by radial thickenings which run for the entire length (Figs 5a,l). At other levels of focus there is a large meshed reticulum (Fig. 5c). Micropunctae on bladder surface (Fig. 5h). Ventral roots of bladders impinge on to furrow but intersection sharp (Fig. 5i). Furrow small-rugulate; punctuated with crater-like depressions (Figs 5h,i,j).

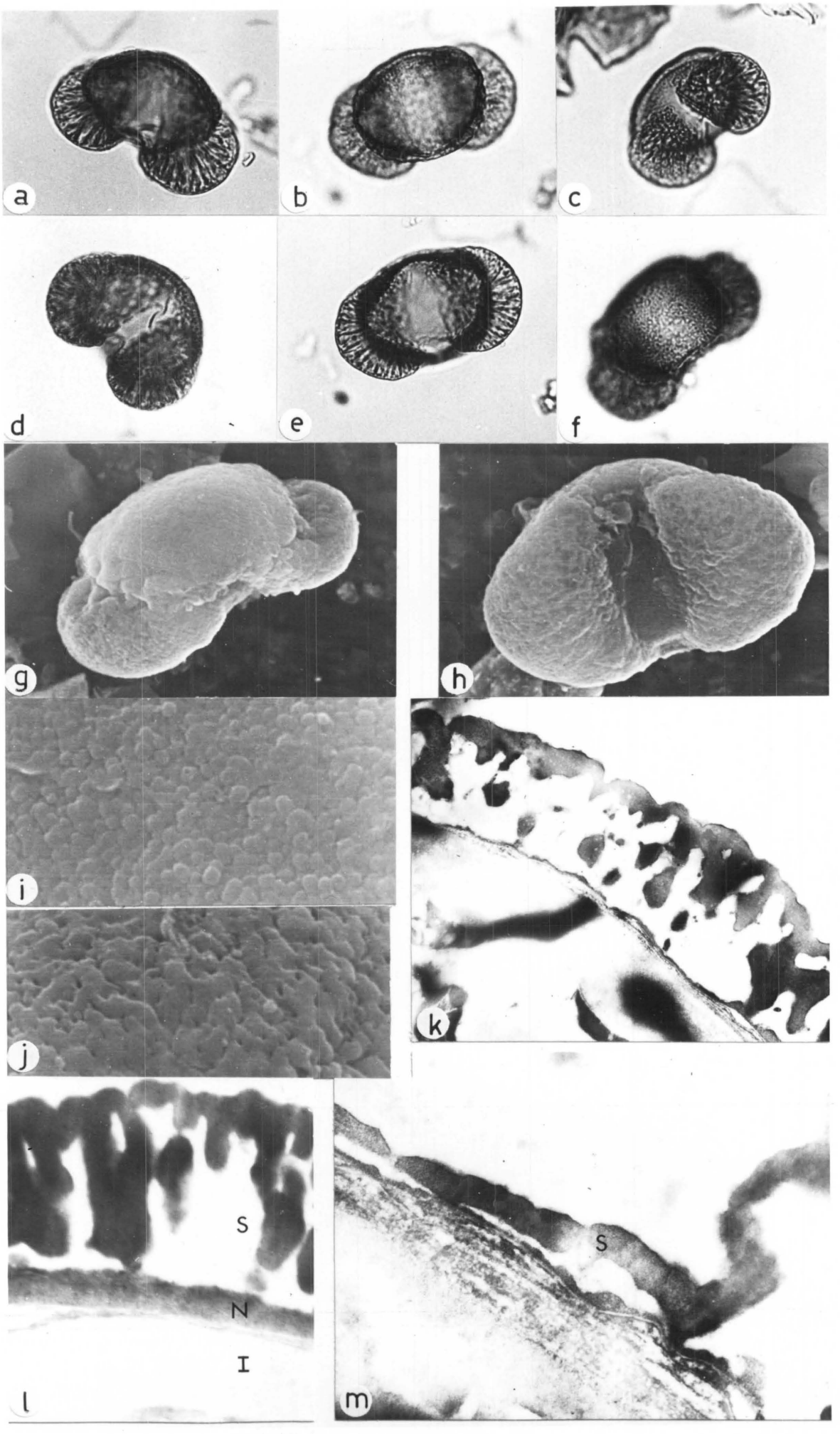
Dacrydium biforme (Hook.) Pilger (pink pine) Figure 6a-k. Cap spheroidal to ellipsoidal; small tuberculate-rugulate (Fig. 6b) in centre becoming differentiated into a thick marginal ridge (Fig. 6h). Exine as in *D. bidwillii*. Bladders hemispherical, sometimes irregular in shape although much sharper outline than in *D. bidwillii* (Fig. 6d). Bladder reticulum (Fig. 6e) similar to *D. bidwillii*. Sharp distinction between bladder and furrow (Figs 6e,g); no furrow rim; furrow has low relief but coarse rugulate sculpturing (Figs 6i,k).

Dacrydium kirkii F. Muell ex Parl. (monoao) Figure 7a-m. Cap ellipsoidal and uniform; small tuberculate (Fig. 7i) in centre but differentiates into a marginal ridge near the dorsal roots of the bladder; sexine thick, large alveolate to columellate (Figs 7k,l). Bladders hemispherical; small (compare *D. bidwillii* and *D. biforme*); attached towards the dorsal side of the grain they project little beyond the corpus in polar views; outline sharp (Figs 7c,e); densely crowded radial thickenings run the entire length (Figs 7a,d); internally thickened meshes give a complex reticulum.

Figure 7. *Dacrydium kirkii.*

a - f Light micrographs (all x 800).
g - j Scanning electron micrographs.
k - m Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (proximal); thick exine.
c. Polar view (distal).
d. Polar view (distal); densely crowded radial thickenings in bladder.
e. Polar view (distal); clearly defined bladders.
f. Polar view (proximal); small tuberculate cap sculpturing.
g. Lateral longitudinal view (x 1700).
h. Polar view (distal); narrow furrow enclosed by bladder (x 1700).
i. Polar view (proximal); small tuberculate cap sculpturing (x 8600).
j. Micropunctae on bladder surface (x 8600).
k,l. Section through tectate cap; large alveolate sexine (S), and thin nexine (N) overlying intine (I) (k x 12000, l x 21000).
m. Section through the point of juncture between bladder and furrow; sexine (S) well developed (X 27000).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Outer surface of the bladders is a myriad of micropunctae (Fig. 7j) with coarse folds in the region of the dorsal and ventral roots (Fig. 7h). Furrow and bladders intersect sharply but no furrow rim. Furrow almost smooth (Fig. 7m).

Specimens of *D. kirkii* were difficult to obtain because of its limited geographical distribution and paucity in herbaria. The species has not been recognised in the fossil record but if it is it may be important in climatic interpretations.

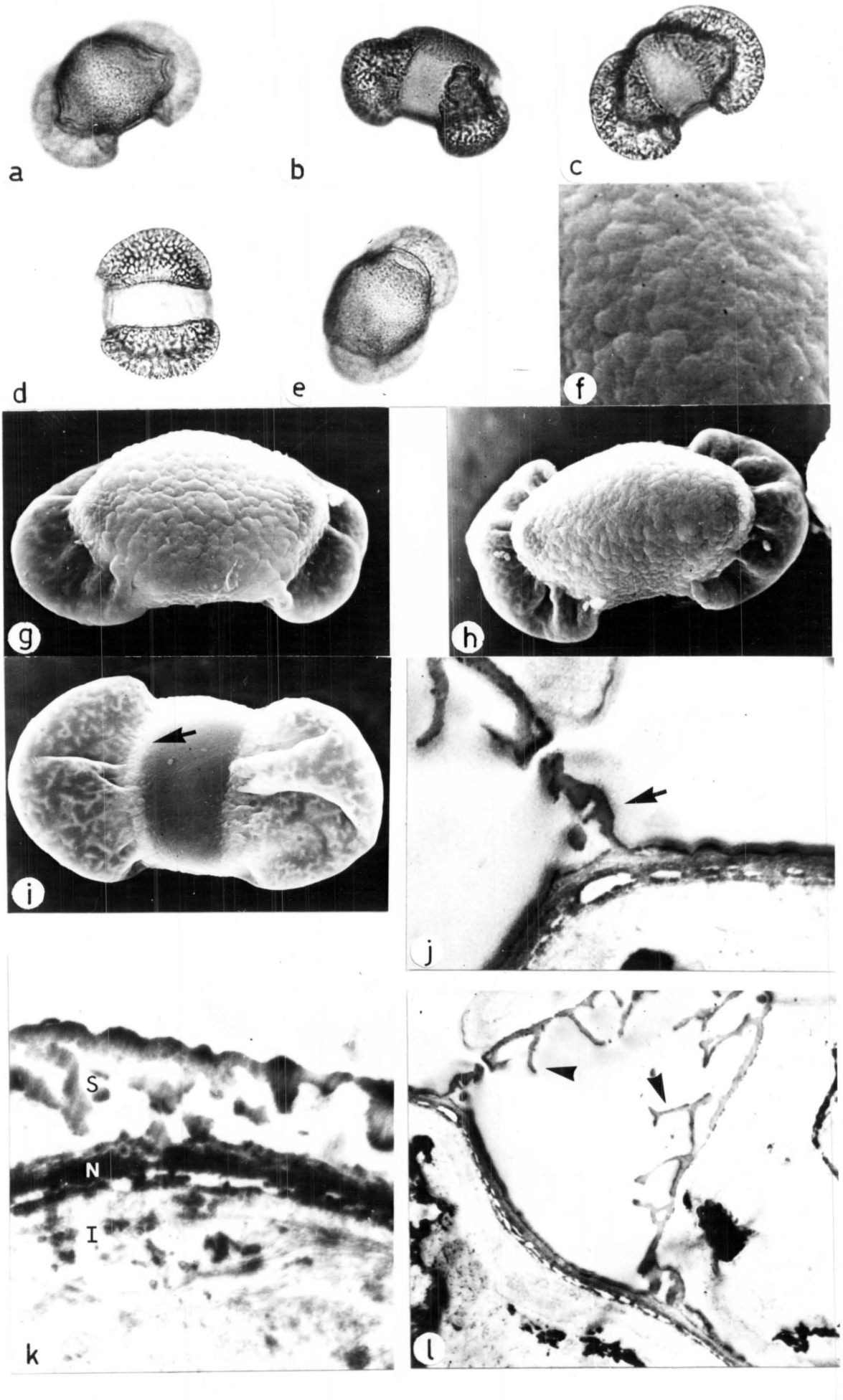
Dacrydium colensoi Hook. (silver pine) Figure 8a-l.
Cap spheroidal to ellipsoidal; finely tuberculate (Figs 8a,e) or large 'cauliflower-type' protrusions similar to some *Podocarpus* spp. (Figs 8f,g); sexine granular to alveolate (Fig. 8k); adjacent to the dorsal roots of the bladders the exine differentiates into a region of 'weakness' (Figs 8e,g,h). Bladders hemispherical (Fig. 8d), not projecting far beyond the cap when fully expanded (Fig. 8b); distinct but delicate reticulum (Fig. 8i) with more-or-less equal, regularly distributed, elongated and polygonal meshes (Fig. 8d); thickened internally (Fig. 8 l) with micropunctae scattered over a smooth surface. Sharp intersection between bladder and furrow (Figs 8b,c,d); distinct furrow rim (Figs 8i,j); furrow finely rugulate (Fig. 8j).

D. colensoi pollen is normally easily identifiable when present in pollen sequences and is well documented in New Zealand Quaternary sediments. Its affinity with *Podocarpus* often causes difficulties in identification but the delicate sculpture of the cap and its bladder reticulation set them apart.

Figure 8. *Dacrydium colensoi.*

a - e Light micrographs (all x 800).
f - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Polar view (proximal); finely tuberculate cap sculpturing.
b. Lateral longitudinal view; sharp intersection between cap and furrow.
c. Polar view (distal).
d. Polar view (distal); clearly defined elongated and polygonal meshes in bladder reticulum.
e. Polar view (proximal).
f. Polar view (proximal); variable cap sculpturing (x 7800).
g. Dorso-lateral view; 'cauliflower type' protrusions on the cap and regions of 'weakness' (x 1500).
h. Polar view (proximal); ellipsoidal body shape and hemispherical bladders (x 1500).
i. Polar view (distal); delicate internal bladder reticulum, furrow rim (arrowed) and smooth furrow (x 1500).
j. Section through furrow rim (arrowed) and rugulate furrow (x 9300).
k. Section through tectate cap; thick, alveolate sexine (S), nexine (N) and intine (I) (x 16000).
l. Section through bladder; infratectal sexinous elements arrowed (x 5100).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Dacrydium laxifolium Hook. f. (pygmy pine) Figure 9a-l. Cap ellipsoidal; small tuberculate-rugulate (Figs 9e,f) but more folded near dorsal margins; sexine thick with well developed columellae (Figs 9j,l). Marginal ridge often distinct (Fig. 9g). Bladders hemispherical (Fig. 9a); turgid with sharp, clear outline; borne on the ventral surface of the corpus and project ventrally and laterally from it. Bladders normally possess numerous folds (Fig. 9b); have a distinct reticulum with unequal irregularly distributed, elongated meshes of various sizes and outlines (Figs 9a,h,i); thickened internally with micropunctae on an uneven outer surface. Furrow and bladders intersect sharply (Figs 9a,i); distinct furrow rim (Fig. 9h); furrow finely rugulate with well developed nexine (Fig. 9k).

Aberrant grains are common (Cranwell 1940) and were also frequently observed in this study. The most prevalent forms consist of completely fused, encircling bladders (Fig. 9c); and one large and one small bladder (Fig. 9d).

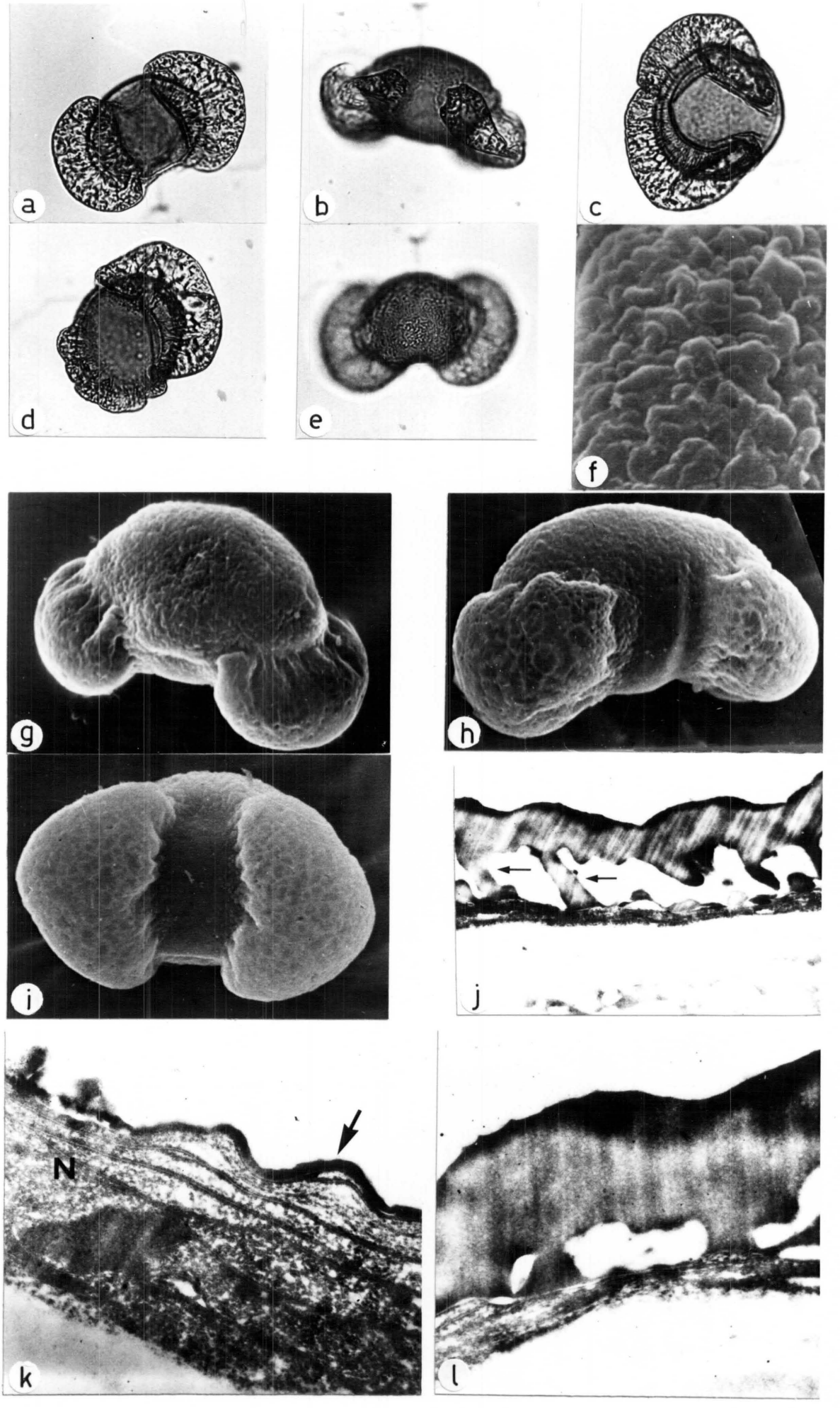
Ueno (1974a) examined pollen of *D. laxifolium* with the scanning electron microscope. His results are very poorly illustrated due to the condition of his sample but he postulated that the tectum (surface) is supported by "baculum like rods" which seem to be more closely spaced at and near the proximal pole. In this study the rods are consistent with tuberculae.

D. laxifolium is not normally recognised in fossil preparations. If it were present its similarity to the *Podocarpus* type (especially *P. spicatus*) probably suggests its placement in pollen diagrams, but this doesn't seem likely as the low, prostrate form of the plant restricts good

Figure 9. *Dacrydium laxifolium.*

a - e Light micrographs (all x 800).
f - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Polar view (distal); unequal, elongated meshes in bladder reticulum.
b. Lateral longitudinal view; bladder folds.
c,d. Polar view (distal); aberrant grains.
e. Polar view (proximal); tuberculate-rugulate cap sculpturing.
f. Polar view (proximal); cap sculpturing (x 10300).
g. Dorso-lateral view (x 1750).
h. Lateral longitudinal view (x 1750).
i. Polar view (distal) (x 1750).
j. Section through tectate cap; columellae (arrowed) well developed (x 10000).
k. Section through furrow; thick nexine (N) and thin rugulate sexine (arrowed) (x 29000).
l. Section through cap (x 32000).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representation in surface and peat samples. The large folded bladders make for relatively safe specific identification.

Dacrydium intermedium Kirk (yellow-silver pine) Figure 10a-j. Cap spheroidal to rhomboidal; weakly tuberculate-rugulate for much of dorsal area (Figs 10b,d,i); tuberculate regions of 'weakness' at the lateral margins near dorsal roots of bladders (Figs 10e,g,i). Bladders hemispherical (Fig. 10c); rigid with clear outline; small compared to corpus but when fully expanded project well beyond the limits of the corpus; small meshed reticulum often interrupted with irregular, varied meshes which are sometimes not distinct because the muri are interrupted (Figs 10c,d); thickened internally. Ventral roots of bladder extend on to furrow but prominent furrow rim (Figs 10a,c,h); furrow rugulate (Fig. 10h).

Aberrant grains are frequent and conform to the type previously described for *D. laxifolium*. Often, however, one bladder may be vestigial (Fig. 10f).

The pollen of *D. intermedium* is not recognised in pollen analysis, perhaps due to its limited geographical distribution and more specialised ecology. It may be confused with the *Podocarpus* type but the nature of bladder reticulation, wide furrow and zones of 'weakness' are important delineating features.

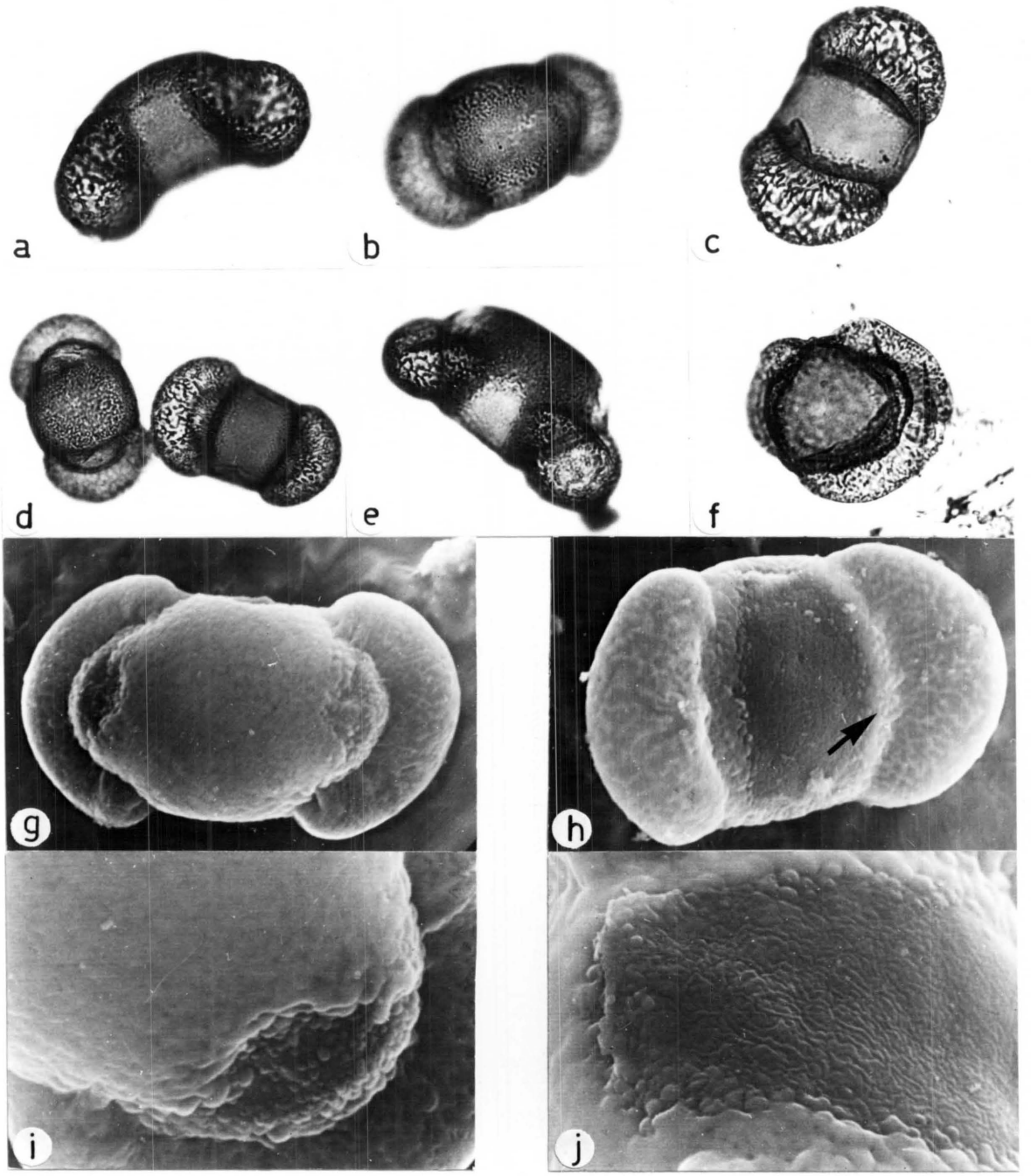
Problems in Identification

The pollen of *Dacrydium cupressinum* is distinctive among the New Zealand *Dacrydium* species. The size of the corpus, the poorly developed bladders with their rough outline combined with the overall coarse tuberculate-rugulate

Figure 10. *Dacrydium intermedium.*

a - f. Light micrographs (all x 800 except as otherwise stated).
g - j. Scanning electron micrographs.

a. Ventro-lateral view.
b. Polar view (proximal); tuberculate-rugulate cap sculpturing.
c. Polar view (distal); interrupted small meshed bladder reticulum and furrow rim.
d. Two grains (x 620).
e. Lateral longitudinal view; sharp distinction between cap and furrow.
f. Polar view (distal); aberrant grain with one large bladder and one small.
g. Polar view (proximal); rhomboidal cap shape and almost sculptureless cap (x 1300).
h. Polar view (distal); furrow rim (arrowed) and shadows of bladder reticulum (x 1300).
i. Polar view (proximal); region of 'weakness' with tuberculate surface (x 3200).
j. Polar view (distal); rugulate furrow (x 3400).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sculpturing set it apart from the other species. Further specific identification must be tentative and the best that can be achieved is the following grouping:

(i) *D. kirkii*, *D. bidwillii*, *D. biforme*

(ii) *D. colensoi*, *D. laxifolium*, *D. intermedium*.

Couper (1953) recognised group (i) which this study supports finding them inseparable on pollen characters except for a marked difference in the size of *D. kirkii* compared with *D. biforme* and *D. bidwillii* (Table 2). Because only one sample of *D. kirkii* was examined any separation on size must be treated cautiously. There are a number of characters in which *D. biforme* and *D. bidwillii* pollen are dissimilar but none occurs consistently enough to warrant undue attention as major diagnostic characters. Cranwell (1940) shows in her sketches that the radial thickenings in the bladders of *D. biforme* are more regularly patterned than those of *D. bidwillii* and that the bladder outline is much sharper. This study has revealed that use of these characters in specific identification would be a dubious practice because both species show extreme variability and resemble each other very closely.

Overall length was measured for two samples of each species (Figures 11, 12) to assess the value of size measurements in differentiation of *D. bidwillii* and *D. biforme* pollen. Much larger sample numbers are probably needed to substantiate the position (Martin 1959), however it can be seen from the results that fluctuation exists within each species and that *D. bidwillii* although on mean length smaller than *D. biforme*, overlaps the lower portion of the range for

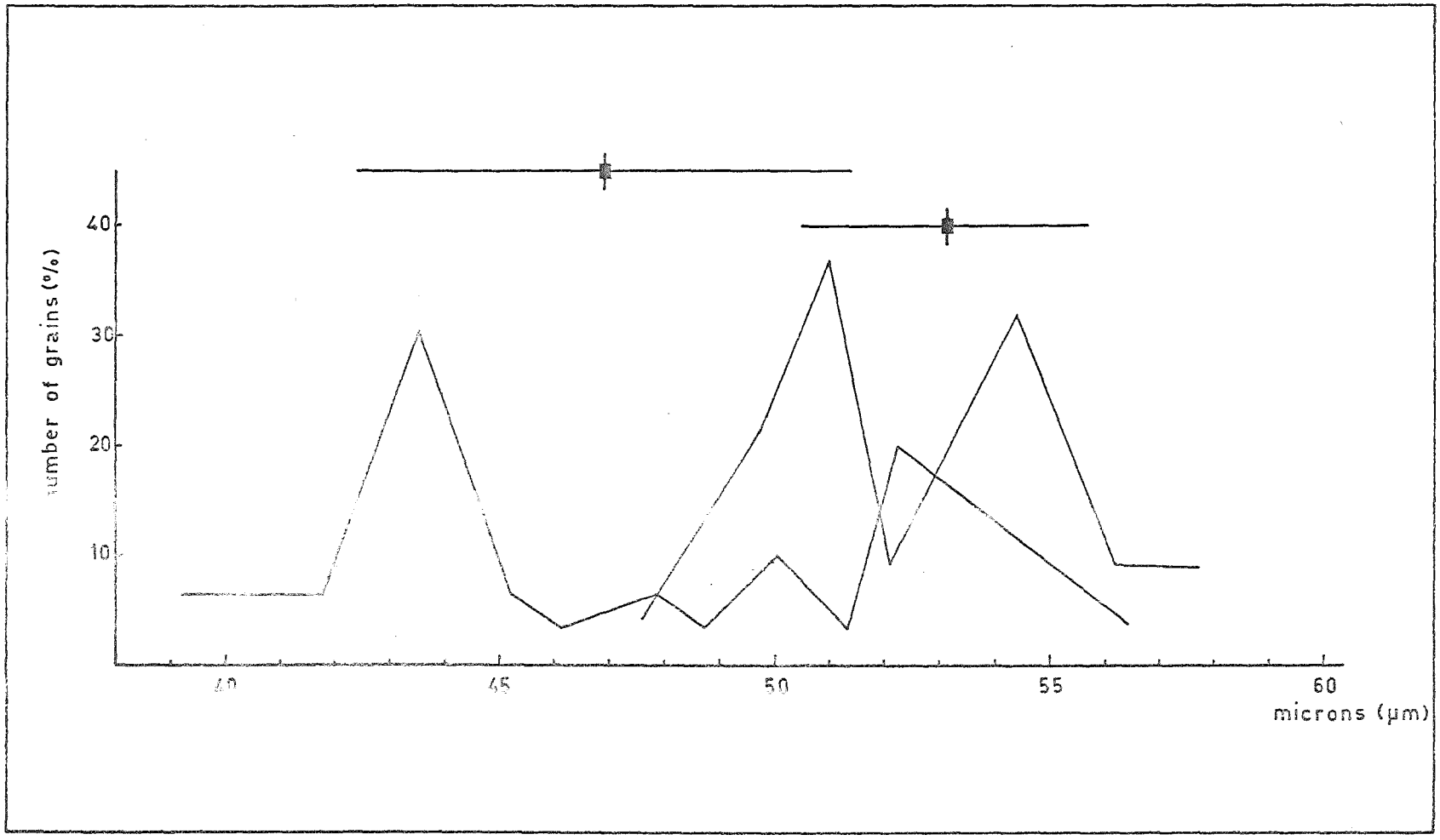


Figure 11. Size frequency distributions for two samples of *Dacrydium bidwillii* pollen measured in silicone oil; short vertical lines = positions of means, thick horizontal lines = standard error either side of means, thin horizontal lines = standard deviation either side of means.

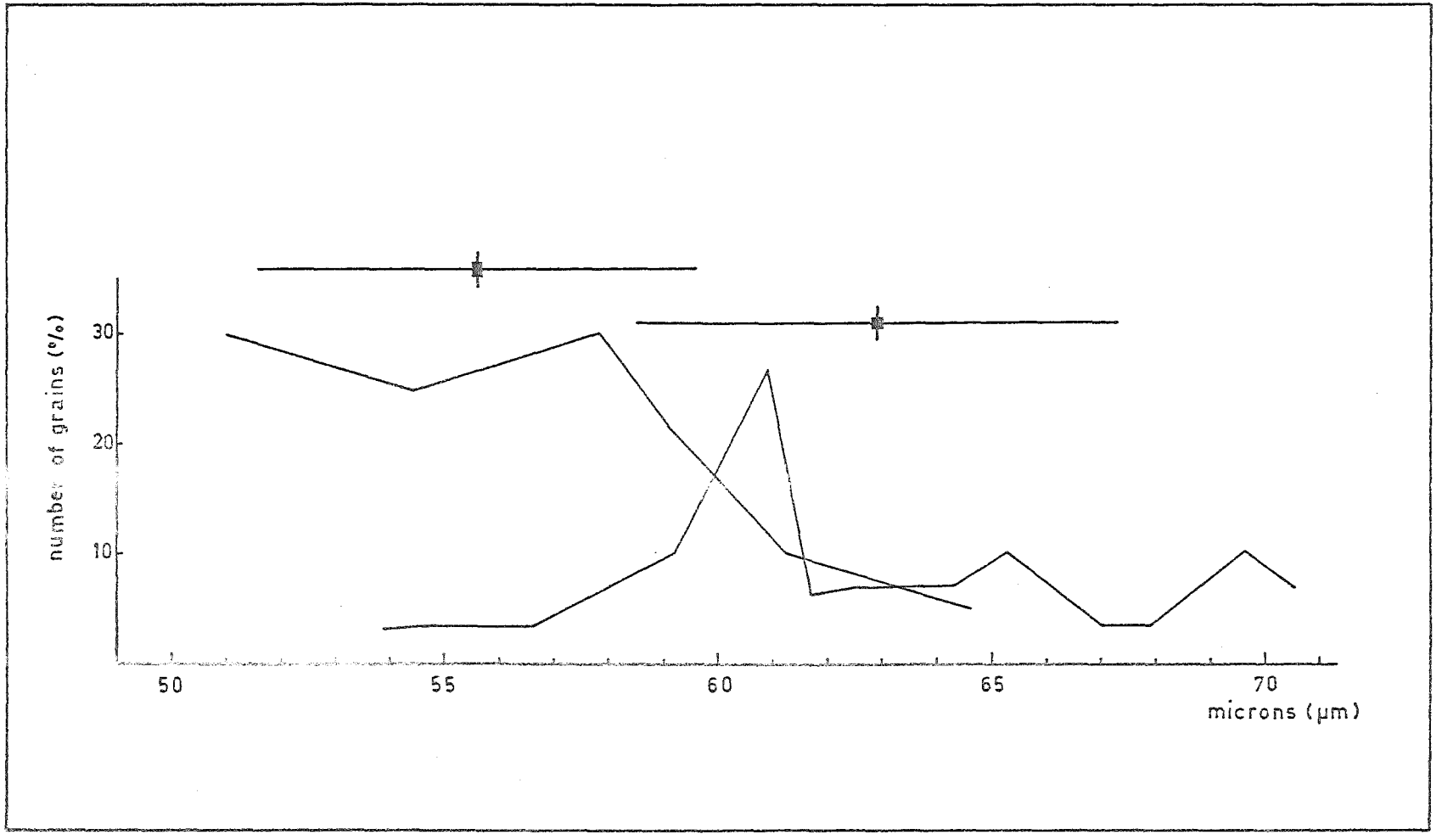


Figure 12. Size frequency distributions for two samples of *Dacrydium biforme* pollen measured in silicone oil; short vertical lines = positions of means, thick horizontal lines = standard error either side of means, thin horizontal lines = standard deviation either side of means.

D. biforme. At the upper and lower extremes it may be safe to make specific identifications (e.g. size >65 µm then probably *D. biforme*), but this can only be tentative. Consequently size calculations provide a tenuous base from which to confidently predict the identity of *D. bidwillii* or *D. biforme* pollen.

Specific identification of *D. bidwillii* and *D. biforme* is difficult. The lack of any definite distinguishing features, combined with possible unfavourable orientation and preservation in fossil material, tend to preclude anything but subjective identification.

The second group of *D. colensoi*, *D. laxifolium* and *D. intermedium* is distinct within *Dacrydium* and very often its members are confused with *Podocarpus* types. The following features distinguish these three species:

(i) distinct bladder reticulation with irregularly distributed, elongated meshes compared to the radial thickenings apparent in group (i) members;

(ii) wide furrow membranes (up to 20 µm in *D. laxifolium*) with a more or less distinct furrow rim;

(iii) regions of 'weakness' which occur on the cap near the dorsal roots of the bladders. These are also seen in the pollen of *Podocarpus spicatus*, *P. ferrugineus* and *Phyllocladus* spp., but have not been reported in previous studies. Their function has not been investigated but it is thought that they may facilitate invagination and thus protect the furrow by closing the bladders during periods of water stress (i.e. harmomegathic function). The grains of these species are often seen in a collapsed state and

those prepared for scanning microscopy may simulate this condition of stress.

Separation within this group lies primarily with differences in cap sculpturing. *D. colensoi* is easily identifiable due to the fine, delicate 'cauliflower-type' protrusions; *D. laxifolium* has tuberculate-rugulate sculptured patterns approaching those exhibited by *D. kirkii*, *D. bidwillii* and *D. biforme*; while *D. intermedium* is finely tuberculate-rugulate or almost sculptureless. In pollen analytical material (peats, mosses etc.) this group is clearly under-represented, perhaps with the exception of *D. colensoi*, so pollen analysts may feel confident that large scale specific identifications of these species are not likely to confront them.

4.2.2 *Podocarpus* L'Heritier ex Persoon

In the genus *Podocarpus* there are about 110 species (Sporne 1971). These are largely confined to forests (lowland and mountain) of warm temperate to tropical countries in the southern hemisphere (Dallimore and Jackson 1966). There are six species and a variety (*Podocarpus totara* var. *waihoensis*) endemic to New Zealand.

Podocarpus is classified into eight sections (Buchholz and Gray 1948) based mainly on leaf anatomy. The most primitive, because its ovules are borne on cones, is section *Stachycarpus*, which contains the New Zealand species *P. spicatus* and *P. ferrugineus* while section *Eupodocarpus* contains *P. totara*, *P. nivalis*, *P. hallii* and *P. acutifolius*. Wood anatomical studies (Kaeiser 1954; Patel 1967b) support the above classification.

Cranwell (1940) studied the pollen of the New Zealand

Table 3. *Podocarpus* and *Dacrycarpus* pollen examined, geographical location, collector and herbarium reference.

TAXON	LOCALITY	COLLECTOR	HERBARIUM REFERENCE
Podocarpus spicatus	Hope Arm, Manapouri, Fiordland	C.J. Burrows	CANU[1] 12755
	Woodstock, Waimakariri River, Canterbury	C.E. Foweraker	CANU 1296
	Orongorongo Valley, Wellington	Unknown	CHR[2] 8201
	Kaweka State Forest, Hawkes Bay	D.T. Pocknall	-
	Evans Road, Harihari, Westland	D.T. Pocknall	-
	Whirinaki State Forest, Ureweras	M.S. McGlone	-
Podocarpus ferrugineus	Hillsborough, North Taranaki	W. Rumball	CANU 5355
	Gillespies Point, near Fox, Westland	P. Wardle	CHR 166503
	Unknown	J.E. Attwood	CHR 23373
	Western Valley Road, Port Levy, Banks Peninsula	B.P. Molloy	CHR 212903
	Poerua State Forest, Westland	D.T. Pocknall	-
Podocarpus totara	Fox, Westland	D.J. Elphick	CANU 12833
	Waihi Gorge, Geraldine, South Canterbury	G.H. Stewart	-
	Rawhiti Farms, Masterton, Wairarapa	D.T. Pocknall	
Podocarpus nivalis	Otira Gorge, Arthurs Pass National Park	D.T. Pocknall	CANU 25251
	Craigieburn Range, Canterbury	T. McIntosh	-
Podocarpus hallii	Christchurch Botanic Gardens, Canterbury	B.P. Molloy	GEOG[3] 210
	Sandy Point Domain, Invercargill, Southland	A.L. Poole	CHR 23872
Podocarpus acutifolius	Lake Rotoiti, Nelson	D.M. Calder	CANU 7341
	Lake Rotoiti, Nelson	D.W. Filmer	CHR 62863
Podocarpus totara var. *waihoensis*	Mount Hercules Scenic Reserve, Whataroa, Westland	P. Wardle	CHR 228231
	Snake Creek, Poerua State Forest, Westland	D.T. Pocknall	CANU 25259
Dacrycarpus dacrydioides	Crows Road, Harihari, Westland	K.D. Smith	-
	Lake Brunner, Westland	W. Mackay	-
	Rawhiti Farms, Masterton, Wairarapa	D.T. Pocknall	-

[1] Department of Botany, University of Canterbury Herbarium

[2] Botany Division, D.S.I.R. Herbarium

[3] Geography Department, University of Canterbury (Slide reference)

Table 4. Summary of pollen measurements,[1] corpus shape and cap sculpturing[2] in *Podocarpus* and *Dacrycarpus*.

TAXON	TOTAL LENGTH		CORPUS BREADTH		BLADDER LENGTH		FURROW WIDTH		CORPUS SHAPE	DORSAL CAP SCULPTURE
	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE		
Podocarpus spicatus	53.0 ± 1.13 (46.9 - 61.2)	55.08 ± 0.76 (51 - 61.2)	30.03 ± 0.60 (27.2 - 34)	31.87 ± 0.67 (27.2 - 37.4)	18.94 ± 0.56 (15.3 - 23.8)	19.38 ± 0.52 (17 - 23.8)	15.05 ± 0.38 (13.6 - 17)	15.55 ± 0.41 (13.6 - 20.4)	Rhomboidal	Tuberculate-rugulate (?)
Podocarpus ferrugineus	71.8 ± 0.99 (60.9 - 85)	88.67 ± 2.02 (78.2 - 107.8)	49.51 ± 0.48 (45.9 - 52.7)	56.44 ± 0.83 (51 - 64.6)	29.41 ± 0.44 (27.2 - 34)	34.73 ± 1.97 (30.6 - 44.2)	16.49 ± 0.44 (11.9 - 20.4)	18.95 ± 0.22 (17 - 22.1)	Ellipsoidal to rhomboidal	Tuberculate-rugulate
Podocarpus totara	53.63 ± 1.06 (44.2 - 61.2)	62.38 ± 0.80 (56.1 - 68)	30.86 ± 0.64 (25.5 - 37.4)	31.62 ± 0.75 (27.2 - 37.4)	19.72 ± 0.38 (17 - 23.8)	22.36 ± 0.35 (20.4 - 23.8)	16.83 ± 0.41 (13.6 - 20.4)	19.04 ± 0.44 (17 - 23.8)	Spheroidal to ellipsoidal	Coarsely rugulate
Podocarpus nivalis	53.21 ± 0.96 (47.6 - 61.2)	63.21 ± 0.99 (54.4 - 71.4)	31.11 ± 9.46 (27.2 - 34)	35.28 ± 0.50 (30.6 - 39.1)	19.04 ± 0.56 (13.6 - 22.1)	25.74 ± 0.40 (22.1 - 28.9)	14.62 ± 0.26 (13.6 - 17)	12.92 ± 0.43 (10.2 - 15.3)	Spheroidal	Rugulate
Podocarpus hallii	52.78 ± 0.89 (47.6 - 57.8)	57.16 ± 0.48 (54.4 - 61.2)	30.68 ± 0.50 (27.2 - 34)	32.42 ± 0.42 (30.6 - 37.4)	19.91 ± 0.38 (17 - 22.1)	22.20 ± 0.51 (20.4 - 27.2)	15.76 ± 0.31 (13.6 - 17)	17.00 ± 0.17 (15.3 - 18.7)	Spheroidal	Rugulate
Podocarpus acutifolius	48.70 ± 0.50 (44.2 - 51)	54.49 ± 0.71 (47.6 - 61.2)	23.12 ± 0.45 (20.4 - 27.2)	26.18 ± 0.36 (23.8 - 28.9)	18.45 ± 0.51 (13.6 - 22.1)	19.77 ± 0.26 (17 - 20.4)	11.98 ± 0.33 (10.2 - 13.6)	13.51 ± 0.15 (11.9 - 15.3)	Spheroidal to ellipsoidal	Coarsely rugulate
Podocarpus totara var. *waihoensis*	54.91 ± 0.44 (52.7 - 61.2)	61.28 ± 0.69 (57.8 - 66.3)	26.69 ± 0.30 (23.8 - 28.9)	34.17 ± 0.56 (27.2 - 37.4)	20.23 ± 0.20 (18.7 - 22.1)	22.78 ± 0.48 (20.4 - 27.2)	16.40 ± 0.25 (13.6 - 17)	16.49 ± 0.32 (13.6 - 18.7)	Spheroidal	Rugulate
Dacrycarpus dacrydioides	59.61 ± 1.18 (51 - 64.6)	72.25 ± 2.11 (51 - 85)	39.21 ± 0.73 (34 - 44.2)	44.8 ± 1.63 (30.6 - 51)	18.81 ± 0.73 (13.6 - 23.8)	27.42 ± 0.69 (23.8 - 34)	24.80 ± 0.67 (23.8 - 27.2)	31.96 ± 2.02[3] (27.2 - 37.4)	Spheroidal	Tuberculate

[1] Mean with standard error followed by range in parenthesis. All measurements in microns (μm).

[2] Only predominant type quoted; other types are discussed in the text.

[3] Triangular furrow of *Dacrycarpus* measured at greatest distance across the furrow.

Podocarpus species and found that those in each section had distinctive pollen morphologies but further subdivision presented difficulties.

A provisional key compiled by Couper (1953) separates *P. spicatus* from *P. ferrugineus* on the reticulation of the bladders while *P. nivalis* is distinguished from *P. totara*, *P. hallii* and *P. acutifolius* on a smaller corpus size. Cranwell (1940) first recognised the importance of pollen of *P. spicatus* and *P. ferrugineus* in our fossil record and thus the need for separation on pollen characters. Her work illustrated irregularities in the cap sculpture of *P. spicatus* but in her final summation she suggested the use of size statistics as a probable medium for delineation. Measurements made on these two pollen types and their probable significance in final determination are discussed in this chapter.

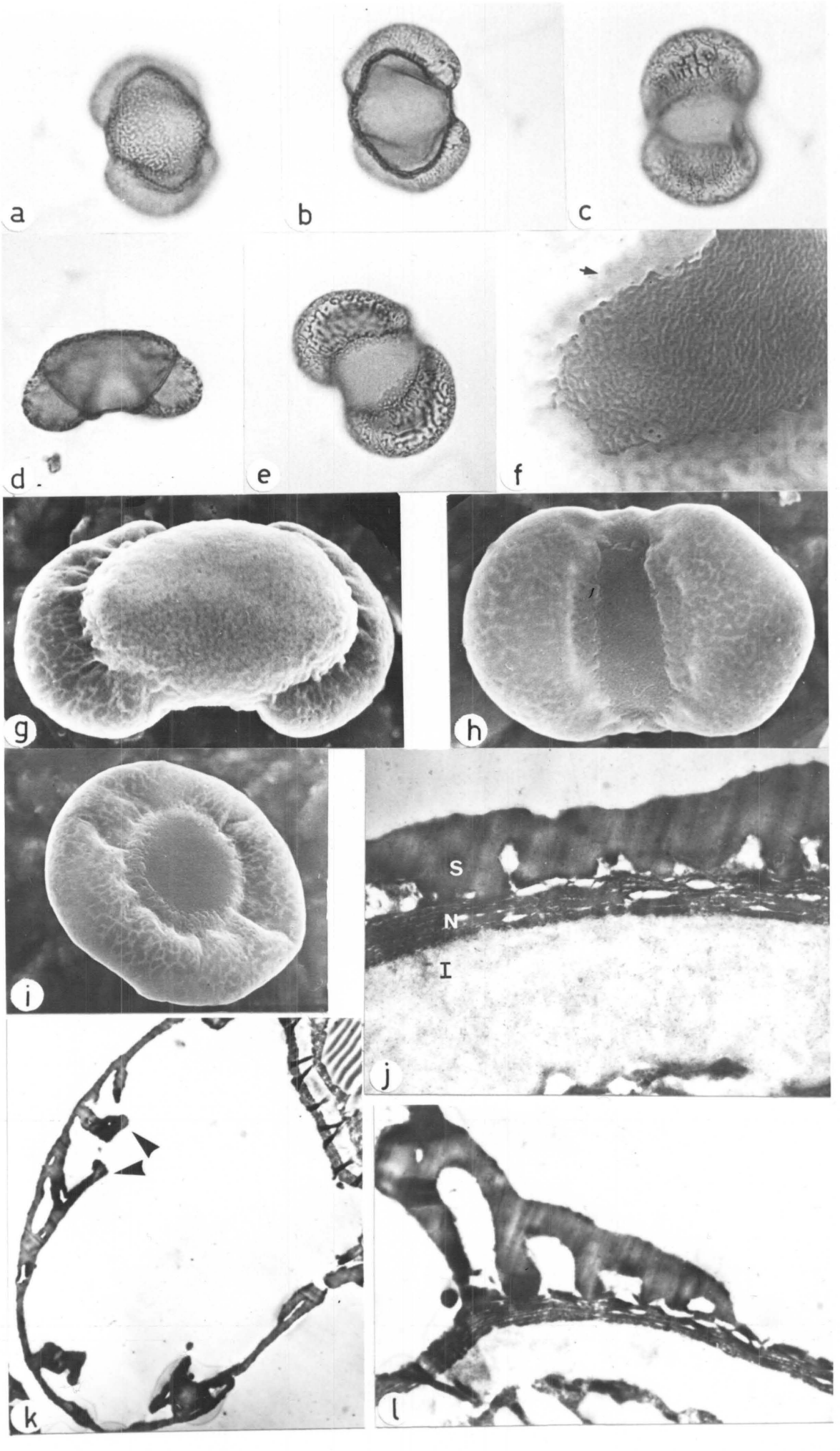
Descriptions of Pollen

Podocarpus spicatus R. Br. ex Mirbal (matai) Figure 13a-l. Cap rhomboidal but does vary; small chagrenate-rugulate (Figs 13a,g) for much of dorsal cap merging into a pronounced marginal ridge; sexine granular to incipiently alveolate over laminated nexine (Fig. 13j); regions of 'weakness' near dorsal roots of bladders. Bladders rounded and hemispherical (Figs 13c,e); may be irregular in outline; flaccid and often collapsed; mostly small, not extending far beyond the corpus in polar view and almost uniting at lateral margins (Figs 13c,h); attached on the ventral side of the corpus and project laterally from it (Fig. 13d); reticulum small meshed, more-or-less distinct forming

Figure 13. *Podocarpus spicatus.*

a - e Light micrographs (all x 820).
f - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Polar view (proximal); small chagrenate-rugulate cap sculpturing.
b. Polar view (proximal); rhomboidal body shape.
c. Polar view (distal); small meshed bladder reticulum.
d. Lateral longitudinal view; small bladders.
e. Polar view (distal).
f. Polar view (distal); furrow rim (arrowed) and rugulate furrow (x 4100).
g. Dorso-lateral view; fine cap sculpturing (x 1600).
h. Polar view (distal); small well defined bladders and distinct furrow rim (x 1600).
i. Polar view (distal); aberrant grain with one fused bladder (x 1100).
j. Section through tectate cap; thick intine (I) is overlain by laminated nexine (N) and partially alveolate sexine (S) (x 16000).
k. Section through bladder; infratectal sexinous elements arrowed (x 4200).
l. Section through furrow rim and furrow (x 12000).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thickened polygons with heavy relief lines (Fig. 13c); thickened internally infratectal sexinous elements (Fig. 13k); numerous micropunctae. Bladders and furrow intersect sharply with a well defined furrow rim (Figs 13f,l); furrow rugulate with occasional crater-like depressions near the ventral roots of the bladders (Fig. 13f).

Pollen is frequently aberrant. The most common forms usually result from modifications of the bladder; either more-or-less confluent bladders (Fig. 13i) or occasionally three bladders of which two are normally united in part.

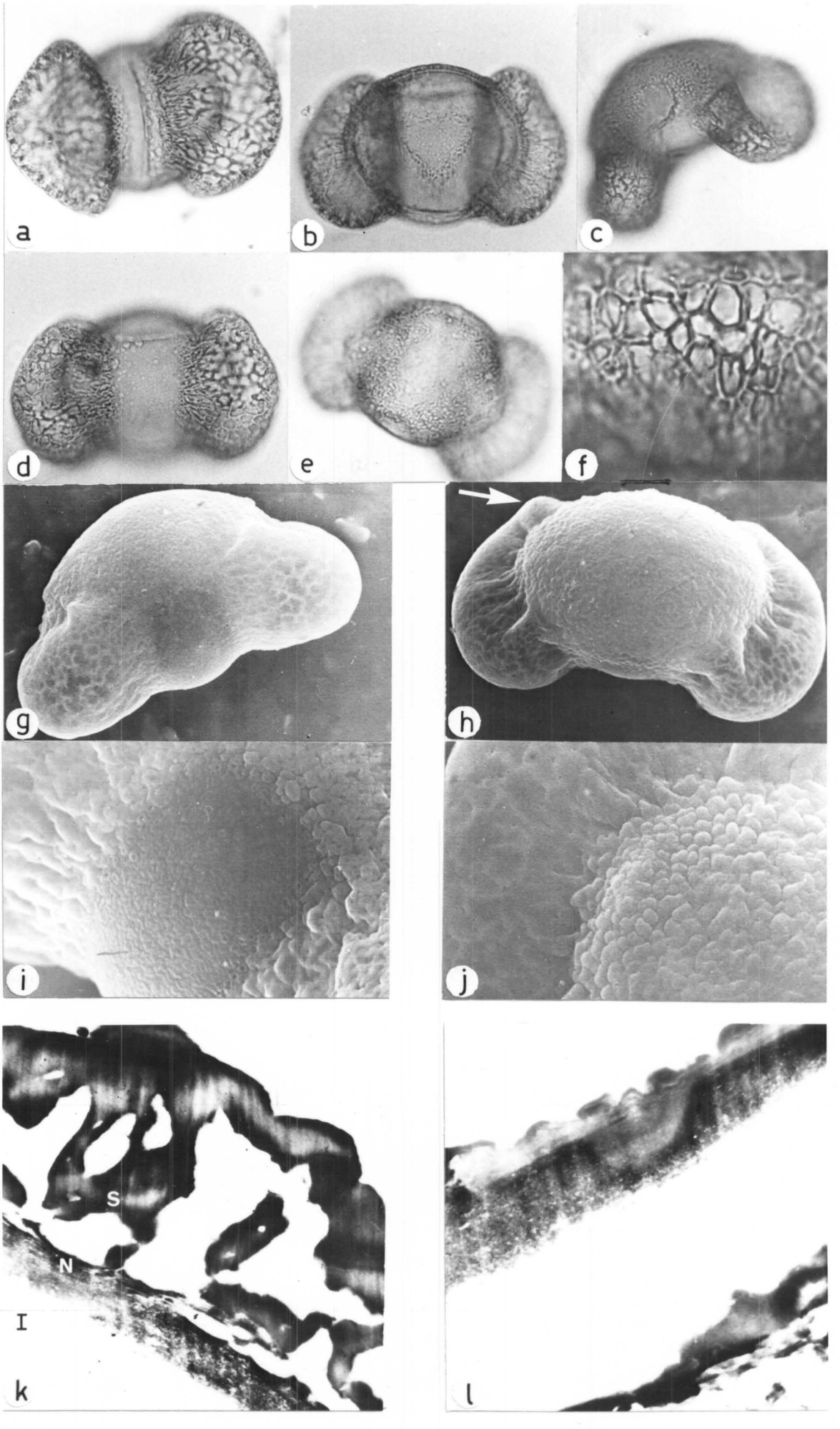
Macko (1957) records *P. spicatus* pollen in Miocene sediments in Poland but the bladders bear no resemblance to those of modern specimens thus doubting this identification. In New Zealand, *P. spicatus* has been grouped in pollen diagrams with *P. ferrugineus* under the title *"Podocarpus"*. Much of the difficulty arises from its orientation in fossil preparations as its limited diagnostic features are sometimes obscured. Bladder reticulation and size are important factors in identification.

Podocarpus ferrugineus G. Benn. ex D. Don (miro) Figure 14a-l. Cap ellipsoidal to rhomboidal; tuberculate-rugulate but in the centre often smooth (Figs 14b,e); region of 'weakness' more tuberculate at cap margin (Fig. 14j); sexine large alveolate (Fig. 14k). Bladders hemispherical (Figs 14a,b); clear outline projecting well beyond the corpus in polar view (Fig. 14d); turgid with large ear-like folds projecting from the dorsal points of junction with the corpus (Figs 14c,h); reticulum large meshed (Fig. 14f), internally

Figure 14. *Podocarpus ferrugineus*.

a - f Light micrographs (all x 675 except as otherwise stated).
g - j Scanning electron micrographs.
k - l Transmission electron micrographs.

a. Polar view (distal).
b. Polar view (proximal).
c. Lateral longitudinal view.
d. Polar view (distal); bladder reticulum blindly branched near ventral roots.
e. Polar view (proximal); tuberculate-rugulate cap sculpturing.
f. Polar view (distal); large meshed bladder reticulum (x 800).
g. Lateral longitudinal view; shadows of bladder reticulum (x 890).
h. Dorso-lateral view; ellipsoidal body shape and ear-like bladder fold (arrowed) (x 1000).
i. Lateral view; small tuberculate-rugulate cap sculpturing and rugulate furrow (x 2800).
j. Polar view (proximal); weakly defined tuberculate marginal ridge (x 2300).
k. Section through tectate cap; thick alveolate sexine (S), laminated nexine (N) and intine (I) (x 13000).
l. Section through rugulate furrow (x 18000).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thickened with heavy relief lines forming a blindly branched system; near bladder roots meshes become elongated in a line running from the point of attachment of the bladder to its periphery (Figs 14a,d); micropunctae numerous appearing consistent with the origin of the infratectal sexinous elements (Fig. 14j). Sharp intersection of bladders and furrow but indistinct and irregular furrow rim (Fig. 14i); furrow rugulate with sexine discontinuous exposing the laminated nexine (Fig. 14 l): occasional crater-like depressions on furrow near bladder roots (Fig. 14i).

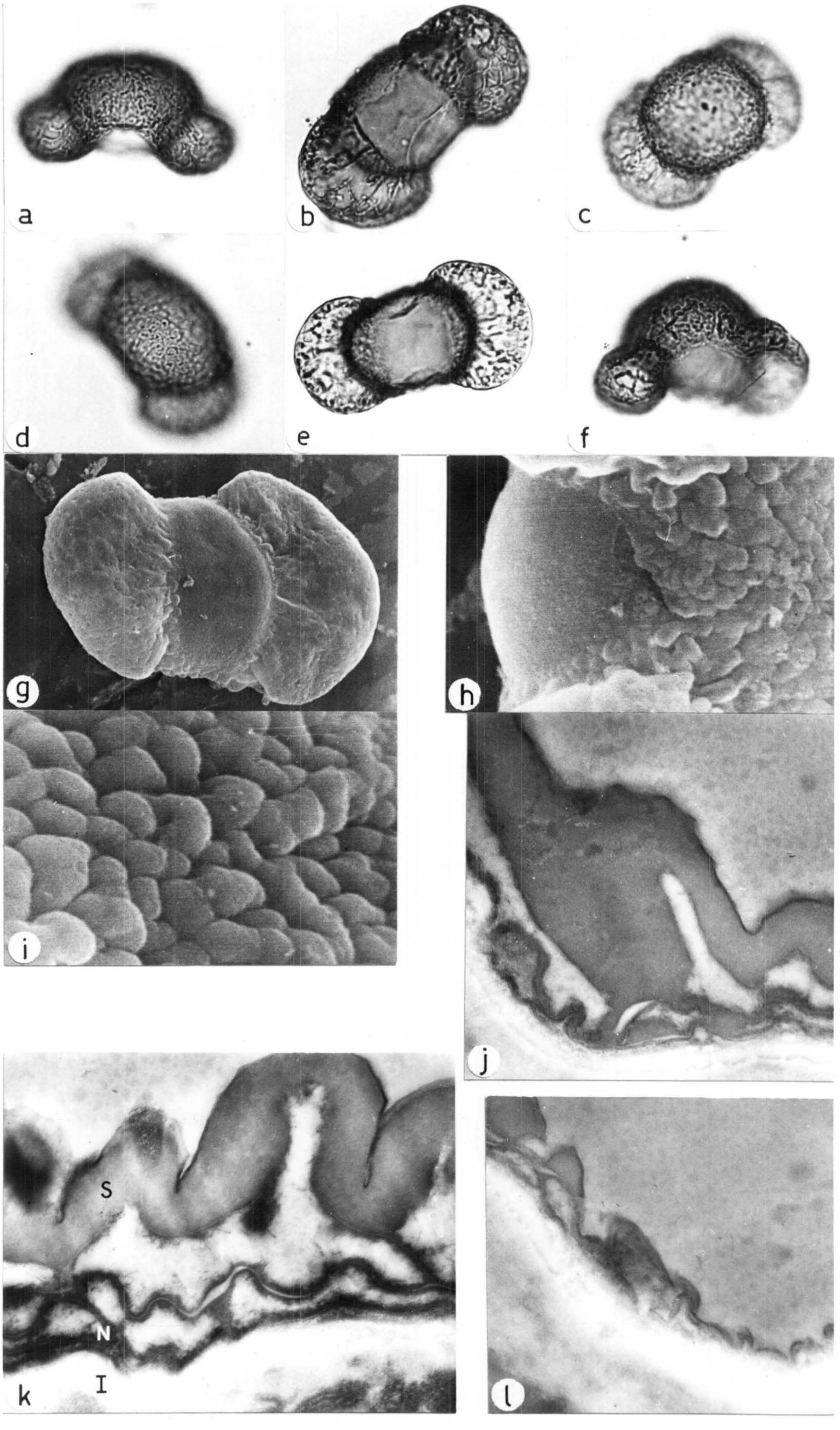
Podocarpus totara G. Benn ex D. Don (totara) Figure 15a-l. Cap spheroidal to ellipsoidal; irregularly small rugulate (Fig. 15i) in middle of dorsal cap but coarsely and unevenly folded near the dorsal roots of the bladders (Figs 15a,c,f); thick collar of exine in optical sections (Fig. 15e); sexine alveolate with nexine consisting only of lamellae (Fig. 15k); suggestion of marginal ridge. Bladders regularly hemispherical (Figs 15b,e); turgid; sharp in outline extending little beyond the corpus in lateral longitudinal section (Fig. 15a); reticulum irregularly large meshed (Figs 15a,b) with heavy well defined relief lines forming strong support for the membrane resulting in perfectly rounded bladders (Fig. 15f); numerous micropunctae (Fig. 15g) and spinules on surface. Bladders and furrow intersect at furrow rim (Figs 15b,g,j); small rugulate furrow (Fig. 15 l).

Pollen of *P. totara* is common in peats but it is often not specifically identified due to its similarity to *P. nivalis*, *P. hallii* and *P. acutifolius* and is therefore grouped

Figure 15. *Podocarpus totara.*

a - f Light micrographs (all x 1075).
g - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (distal); irregularly large meshed bladder reticulum.
c. Polar view (proximal).
d. Polar view (proximal); rugulate cap sculpturing.
e. Polar view (distal); clear bladder outline.
f. Lateral longitudinal view; irregular rugulate cap sculpturing.
g. Polar view (distal); bladders and furrow intersect sharply (x 1700).
h. Lateral view; sharp distinction between cap and furrow (x 4000).
i. Small rugulate cap sculpturing (x 6200).
j. Section through bladder near point of attachment to furrow (x 22000).
k. Section through tectate rugulate cap; sexine (S) overlies nexine (N) and intine (I) (x 26000).
l. Section through furrow; finely rugulate (x 22000).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under the broad title of *"Podocarpus"* type. The bold, thick exine is the normal prerequisite for inclusion into the above group and often it is the only well preserved part of the grain leaving no alternative but to its inclusion in this broad group. Other features such as bladder size, shape and reticulation delineate this group but this is really only applicable to fresh, favourably orientated grains. The provisional key compiled at the end of this chapter uses these features for tentatively identifying *P. totara* pollen but final separation from *P. hallii* is achieved on the basis of irregularity in cap sculpturing.

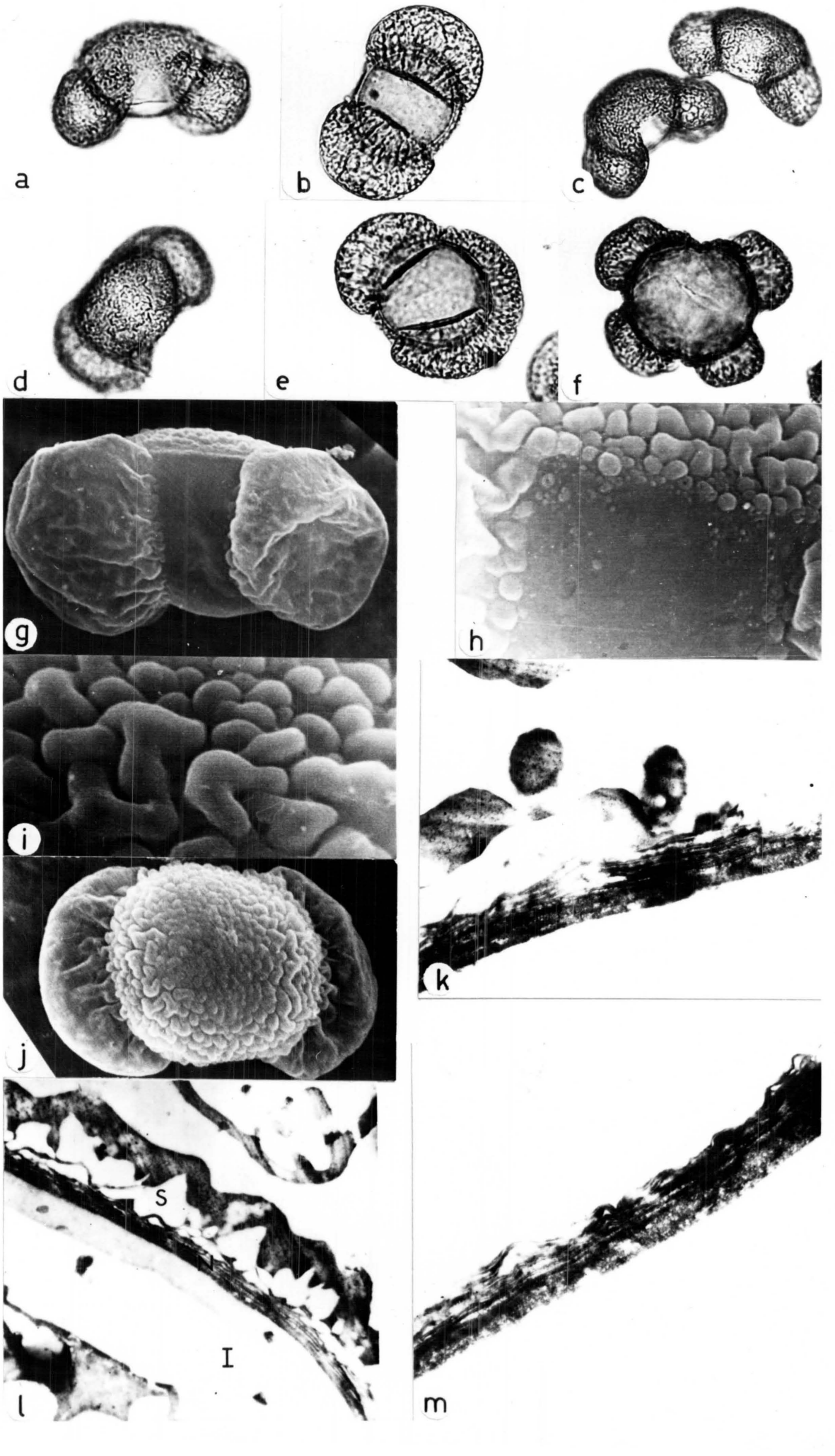
Podocarpus nivalis Hook. (snow totara) Figure 16a-m. Cap spheroidal; coarsely rugulate over much of cap but occasionally interrupted by isolated tuberculae (Figs 16a,d,i,j); sexine alveolate with isolated columellae (Fig. 16 l). Bladders hemispherical (Fig. 16b); clear in outline; variable in size and may extend far beyond the corpus; attached high on the dorsal side of corpus and project laterally from it (Fig. 16c); distinctly folded in region of dorsal roots; internal thickenings diffuse and confused forming a delicately meshed reticulum (Figs 16b,e); isolated micropunctae and small spinules. Sharp intersection delimits bladders and furrow with a distinct furrow rim (Fig. 16b); small folds signify the ventral roots of the bladders; cap sculpturing tuberculate at junction with furrow (Figs 16h,k); furrow rugulate composed of nexine layer only (Fig. 16m), or smooth (Figs 16g,h).

In this study there was a high frequency of morphologically aberrant grains which supports earlier

Figure 16. *Podocarpus nivalis*.

a - f Light micrographs (all x 1075 except as otherwise stated).
g - j Scanning electron micrographs.
k - m Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (distal); bladder reticulum diffuse and delicately meshed.
c. Lateral longitudinal view (x 600).
d. Polar view (proximal); rugulate cap sculpturing.
e. Polar view (distal); aberrant grain with one fused bladder.
f. Polar view (proximal); two grains united.
g. Polar view (distal); bladders partially collapsed with shadows of reticulum (x 1550).
h. Small tuberculae at the junction between cap and furrow (x 3400).
i. Rugulate cap sculpturing (x 6800).
j. Polar view (proximal); spheroidal body shape (x 1550).
k. Section through cap and furrow (refer h) (x 18000).
l. Section through tectate rugulate cap; alveolate sexine (S), laminated nexine (N) and intine (I) (x 8400).
m. Section through furrow; sexine poorly developed (x 19000).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observations made by Cranwell (1940). There are many varied types observed and some are illustrated in Figures 16e,f.

In a provisional key Couper (1953) separated *P. nivalis* from the other members of the group on the basis of a difference in the size of the main body of the grain. This study has revealed no such difference and cannot therefore support Couper's separation but it must be taken into account that his measurements were made *via* the direct method. Cranwell (1940) suggests the similarities within the group but notes that the overall measurement is usually greater in *P. nivalis* and this is often more than twice the average length of the grain. The present study does not support this conclusion. It will be shown later that the most definite difference between *P. nivalis* and the other types is its very diffuse bladder reticulation.

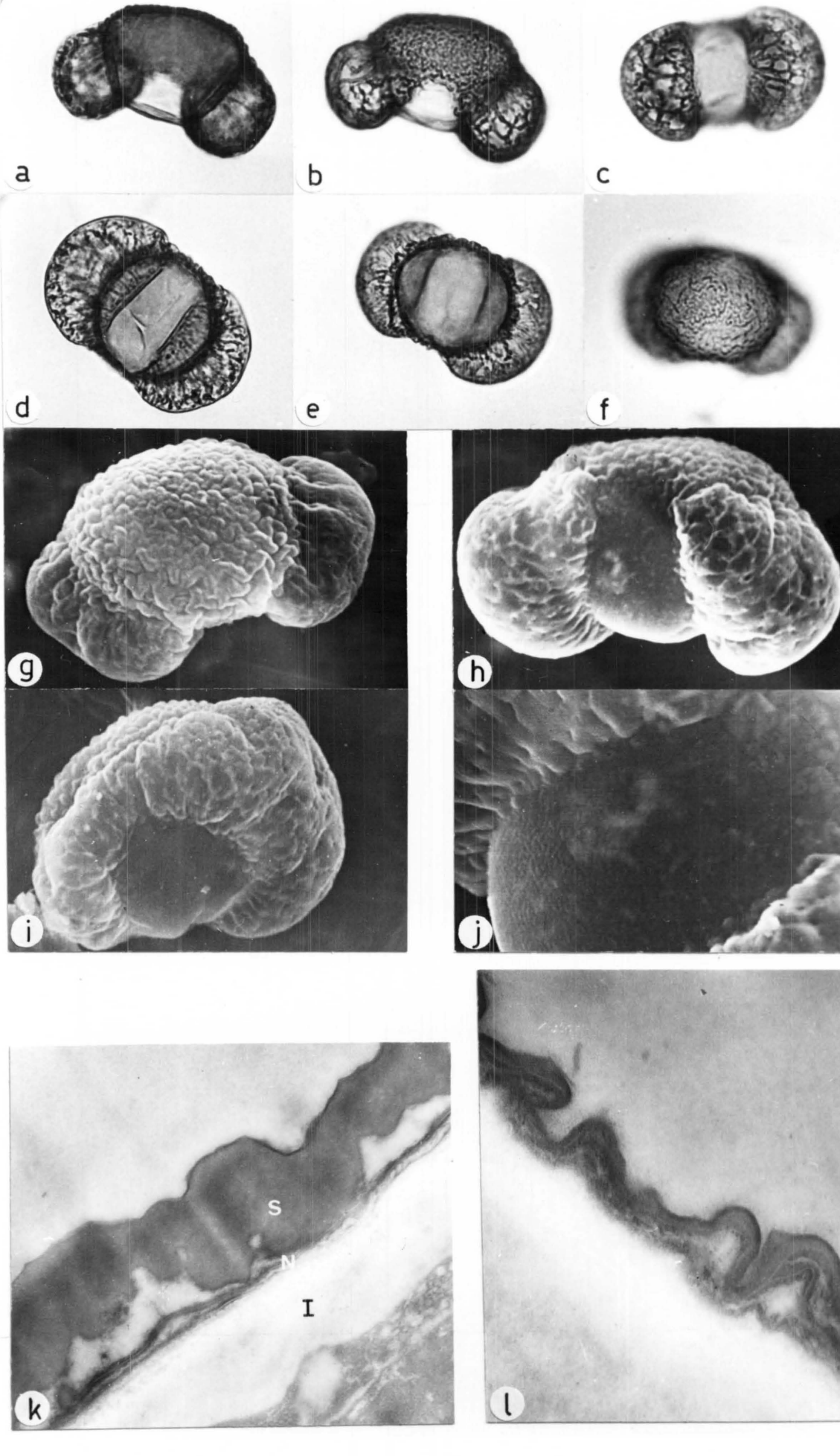
Podocarpus hallii Kirk Figure 17a-l.

Cap spheroidal (more so than in *P. totara*); rugulate over entire cap (Figs 17b,f,g); sexine almost completely granular overlying thin nexine composed of lamellae only (Fig. 17k); margins of cap convoluted into a weakly defined marginal ridge; often elongate rugulae appear continuous with the bladder meshes (Fig. 17b). Bladders hemispherical (Fig. 17d); variable in size; turgid and occasionally lobed; attached more to the centre of the corpus with pronounced dorsal roots (Fig. 17g); reticulum distinct with heavy relief lines, elongated meshes near the ventral roots and smaller meshes near the periphery (Figs 17c,d,h); internally thickened with micropunctae and spinules on the surface (Fig. 17h). Sharp intersection between bladder and furrow

Figure 17. *Podocarpus hallii*.

a - f Light micrographs (all x 1075).
g - j Scanning electron micrographs.
k - l Transmission electron micrographs.

a. Lateral longitudinal view.
b. Lateral longitudinal view; sharp distinction between cap and furrow.
c. Polar view (distal); clear bladder reticulation with heavy relief lines.
d. Polar view (distal); clear bladder outline.
e. Polar view (proximal); thick exine.
f. Polar view (proximal); rugulate cap sculpturing.
g. Dorso-lateral view; rugulate cap (x 1700).
h. Lateral longitudinal view; bladder reticulum clearly defined (x 1700).
i. Lateral view; aberrant grain with one fused bladder (x 1700).
j. Furrow; rugulate sculpturing (x 4300).
k. Section through cap; sexine (S), nexine (N) and intine (I) (x 20000).
l. Section through furrow (x 39000).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with distinct rim (Figs 17d,j); furrow smooth to rugulate (Figs 17j,l).

The study of this pollen was restricted by poor flowering, in the period this study was undertaken, and limited herbarium specimens so the description must be tentatively treated until more specimens are studied. Aberrant grains were noted and usually possessed fully encircling confluent bladders (Fig. 17i).

Cranwell and von Post (1936) suggest that pollen of *P. hallii* is no doubt present in many peats but it has not been recognised as such because of its similarity to *P. totara*. Surface sample analysis in Chapter 6 shows that *P. hallii* pollen is well recorded near source plants but its overall representation is affected by the relative pollen production of the plants it is associated with. It is suggested from its frequent state of collapse in scanning electron microscope preparations that *P. hallii* pollen is delicate and may therefore be poorly preserved in fossil samples. Identification is also impeded by hybridisation of *P. hallii* with *P. nivalis* at higher altitudes and with *P. acutifolius* at lower altitudes which tends to produce a variety of pollen forms which are slightly different when compared with the original *P. hallii* type. Final identification rests with bladder reticulation.

Podocarpus acutifolius Kirk Figure 18a-l.

Cap spheroidal to ellipsoidal; coarsely rugulate (Figs 18e,g,h) with spinules (Fig. 18f); occasional rugulae are elongate and traverse the cap; near junction with furrow cap becomes tuberculate (Figs 18e,j); sexine variable from

large alveolate to columellate (Fig. 18k). Bladders hemispherical (Figs 18b,c,i), but often distorted (Figs 18d,g) and unequal in size; flaccid and collapse easily; attached high on the dorsal side of the corpus and project laterally (Figs 18a,h); reticulum clearly defined but sparse (Fig. 18b); meshes infrequent, only internally thickened relief lines predominate running in a line from the point of attachment to the periphery (Figs 18b,c); micropunctae numerous (Fig. 18i). Ventral roots of the bladders impinge on to furrow giving an irregular intersection and indistinct furrow rim (Fig. 18i); furrow normally sculptureless but infrequent rugulae (Fig. 18 l).

Limited distribution and lack of significant identification features have probably resulted in the low recognition of *P. acutifolius* in pollen profiles. The following features make *P. acutifolius* distinct from *P. totara*, *P. nivalis* and *P. hallii*:

(i) generally smaller than most;

(ii) clear bladder reticulation but sparse in distribution;

(iii) indistinct furrow - bladder junction;

(iv) tuberculate sculpturing of cap subjacent to furrow membrane; and

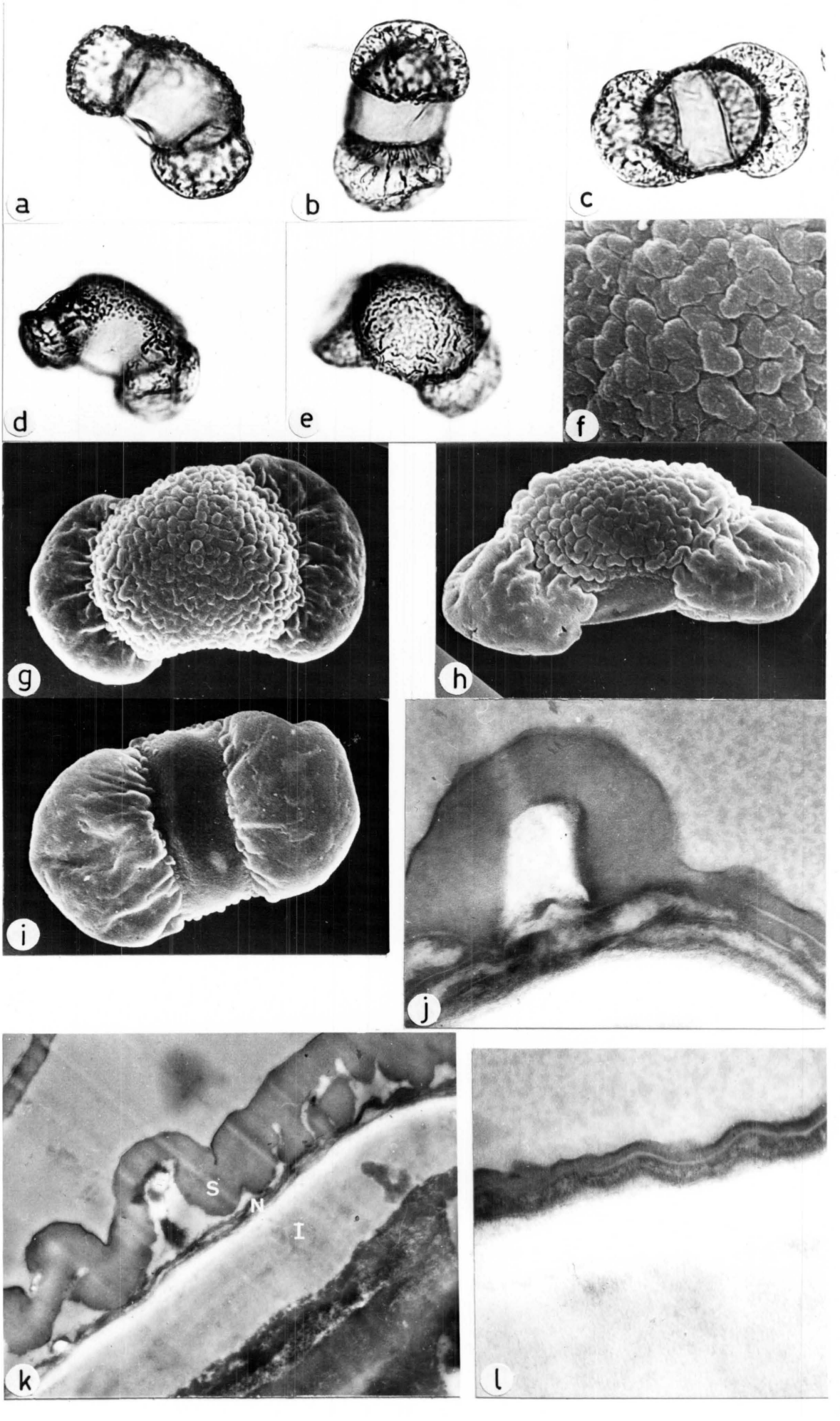
(v) often coarse rugulate sculpturing in middle of cap as well as elongate rugulae.

Cranwell (1940) says that *P. acutifolius* is easily identified but it is worth pointing out that her drawing (p. 10) is thoroughly misleading especially with reference to the bladder reticulation. Couper (1953) grouped *P. acutifolius* with *P. totara* and *P. hallii* but Cranwell's work and this study tend to disagree with Couper's grouping.

Figure 18. *Podocarpus acutifolius.*

a - e Light micrographs (all x 1075).
f - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (distal); clearly defined bladder reticulum.
c. Polar view (distal).
d. Lateral longitudinal view; cap tuberculate at junction with furrow.
e. Polar view (proximal); cap sculpturing of elongate rugulae.
f. Rugulate cap sculpturing with spinose surface (x 3300).
g. Polar view (proximal); bladders partially collapsed (x 1300).
h. Lateral longitudinal view (x 1300).
i. Polar view (distal); smooth furrow (x 1300).
j. Section through the junction of cap and furrow (x 39000).
k. Section through rugulate cap, alveolate sexine (S), nexine (N) and intine (I) (x 9800).
l. Section through furrow (x 45000).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Podocarpus totara G. Benn ex D. Don var. *waihoensis* Wardle

Figure 19a-k.

Cap spheroidal; exine thick (Fig. 19d) similar to *P. totara*; irregularly rugulate with elongate rugulae prominent (Figs 19b,g,h) on outer margins but often finely rugulate in centre of cap (Figs 19b,j); fine spinules on surface of rugulae (Fig. 19h); sexine granular with small alveoli (Fig. 19i). Bladders hemispherical (Figs 19c,d); flaccid; clear in outline; small and equal in size but occasionally lobed at the margins; attached high on the dorsal side of the corpus projecting laterally and horizontally (Figs 19e,f) not far beyond the corpus in lateral longitudinal and polar views; reticulum varies from confused network of poorly defined meshes (Fig. 19c) to one in which the meshes are clearly marked but not completely meshed (Figs 19a,e), as in *P. acutifolius*; internally thickened with numerous micropunctae (Fig. 19f). Bladders and furrow intersect sharply with an obvious furrow rim (Figs 19c,f); furrow smooth, consisting of lamellate nexine (Fig. 19k).

The pollen of *P. totara* var. *waihoensis* has features of both of its parents but appears more closely related to *P. acutifolius*. This makes specific identification difficult. These features are very regular, especially bladder shape, size and position of attachment to the body of the grain and further diagnoses rest in this region of the pollen morphology.

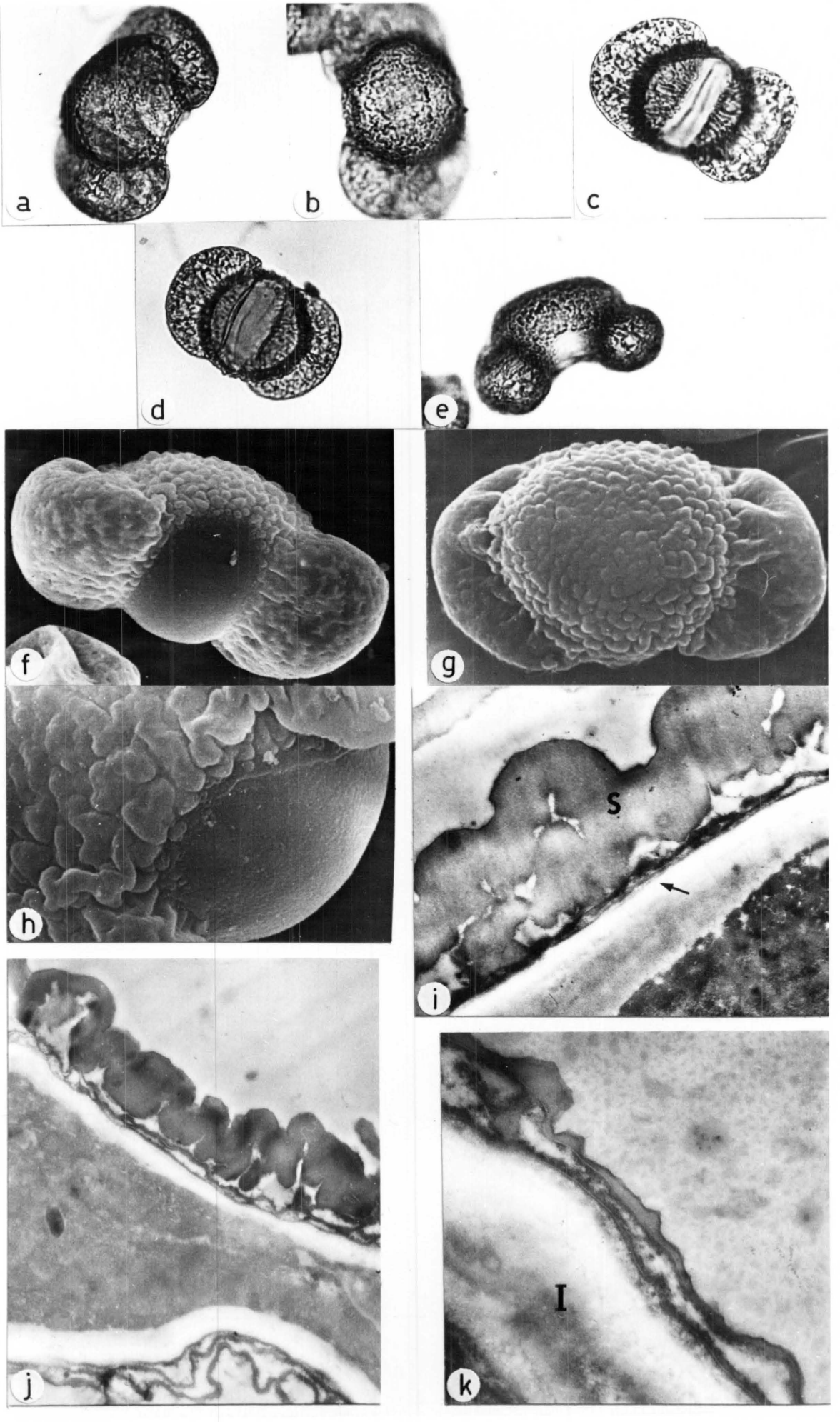
Identifications based on Pollen Morphology

Podocarpus can be separated by pollen characters into two distinct groups. These correlate with the classification

Figure 19. *Podocarpus totara* var. *waihoensis*.

a - e Light micrographs (all x 1075).
f - h Scanning electron micrographs.
i - k Transmission electron micrographs.

a. Dorso-lateral view.
b. Polar view (proximal); rugulate cap sculpturing.
c,d. Polar view (distal); bladder reticulum a confused network of meshes.
e. Lateral longitudinal view.
f. Lateral longitudinal view; micropunctae on bladder (x 1300).
g. Polar view (proximal); rugulate cap sculpturing (x 1600).
h. Lateral view; sharp distinction between rugulate cap and smooth furrow (x 3400).
i. Section through tectate cap; rugulate sexine (S) and thin nexine (arrowed) (x 14000).
j. Section through cap; rugulate sculpturing (x 9200).
k. Section through furrow; thick intine (I) overlain by thin exine (x 27000).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of sections proposed by Buchholz and Gray (1948) and are:

(i) *P. spicatus*, *P. ferrugineus*

(ii) *P. totara*, *P. nivalis*, *P. hallii*, *P. acutifolius*, *P. totara* var. *waihoensis*

Bladder reticulation and size are important factors in differentiating between the pollen of *P. spicatus* and *P. ferrugineus*. In addition, *P. ferrugineus* possesses characteristic ear-like folds which project from the dorso-lateral points of junction between the bladder and the grain and *P. spicatus* exhibits a clearly defined furrow rim. The sculpturing of the cap in *P. spicatus* was reported by Cranwell (1940) to be irregular. This study has revealed wide variation and the feature cannot be considered of diagnostic importance. In both species the reticulum of the bladders is meshed but in *P. spicatus* the meshes are smaller and form more regular, complete polygons. For this reason pollen of *P. spicatus* and *Dacrydium colensoi* are often confused. Couper (1953) used bladder reticulation as a means of differentiating between *P. spicatus* and *P. ferrugineus*.

Another important feature separating the two species is the overall length measurement. Results are presented in Figure 20 which clearly show that *P. ferrugineus* is consistently larger than *P. spicatus*, a feature expected to be adequately portrayed in fossil preparations. Two specimens for each species were examined and the overall length measured on 30 grains per sample. Past references to size are made by Cranwell (1940) whose quoted size ranges suggest that there is little or no overlap between *P. spicatus* and *P. ferrugineus*; Martin (1959) comments that Cranwell's figures appear to show superficially little variability when

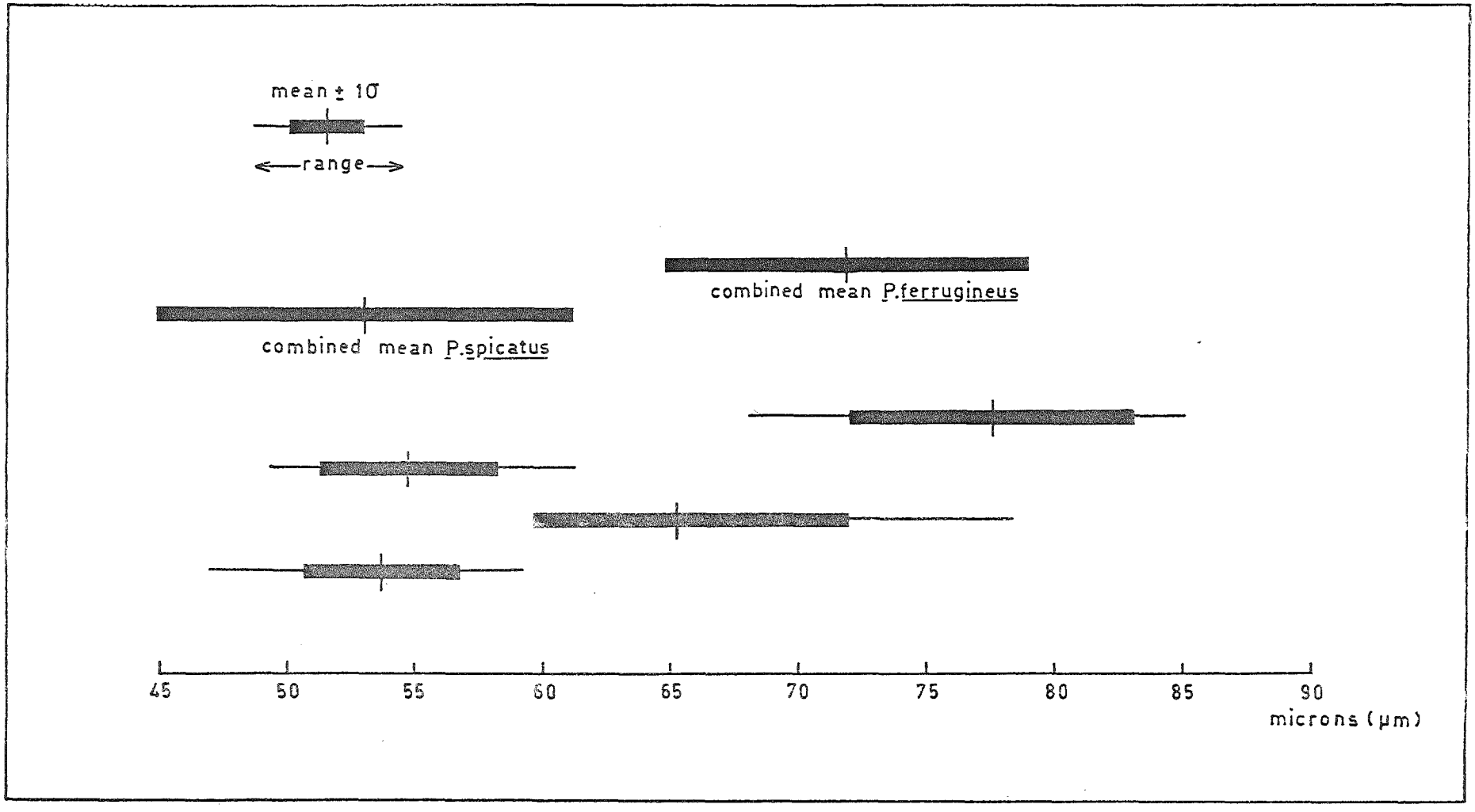


Figure 20. Size distribution of *Podocarpus spicatus* and *P. ferrugineus* pollen measured in silicone oil, showing mean overall length, size range and standard deviation.

compared to South African *Podocarpus* species. It can be stated on the basis of the present results that grains >65 µm (in silicone oil) are *P. ferrugineus* while those >60 µm but <65 µm suggest a degree of uncertainty in their identification. In these examples it is hoped that the other less definite distinguishing features will be favourably preserved, and displayed to facilitate further identification.

4.2.3 *Dacrycarpus* Endlicher

Dacrycarpus is considered an advanced section of the genus *Podocarpus* (Sporne 1971) but some authors (e.g. De Laubenfels 1969) separate it from *Podocarpus* and give it genus status.

Description of Pollen

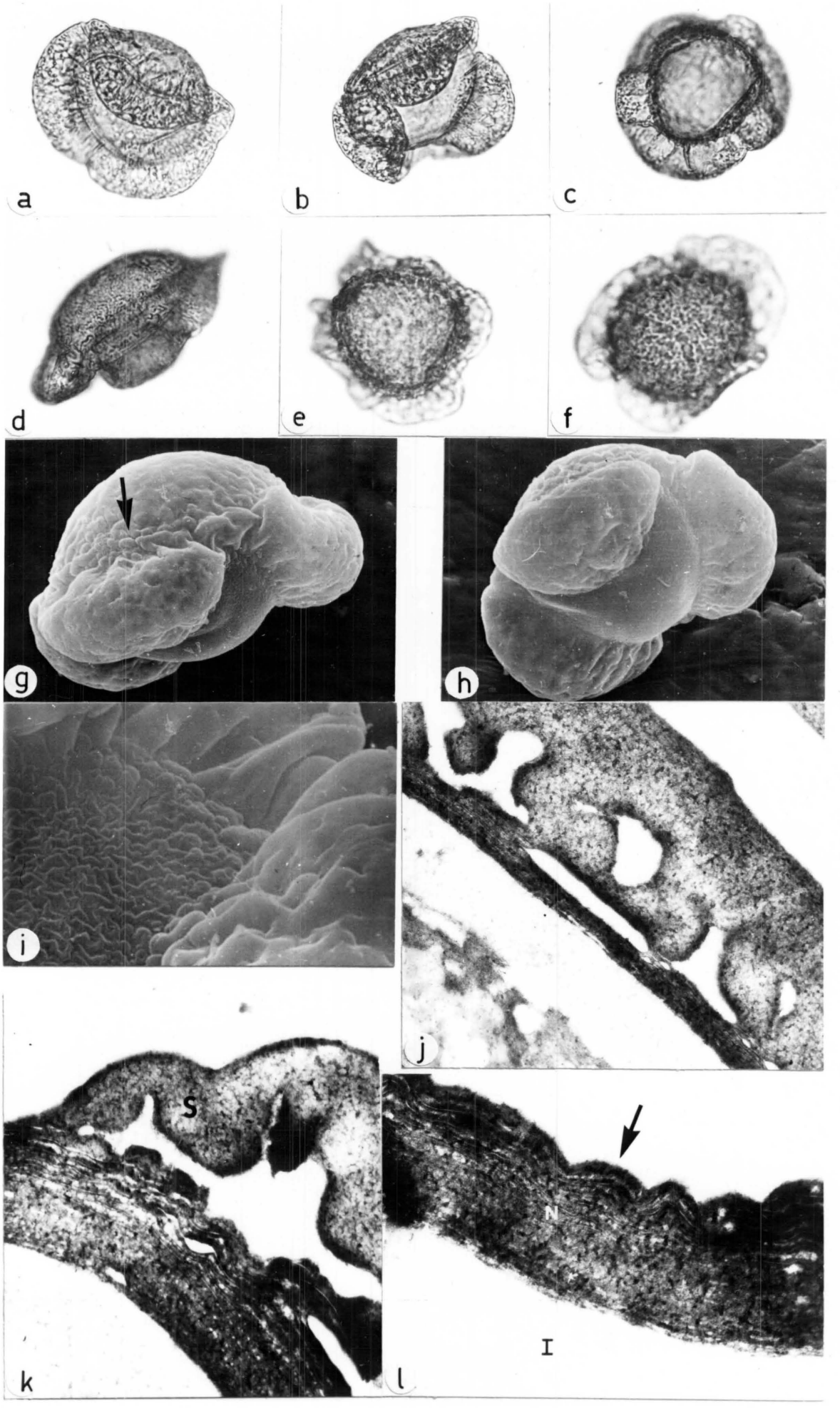
Dacrycarpus dacrydioides (Rich.) de Laubenfels (kahikatea) Figure 21a-l.

Cap spheroidal or lens-shaped in lateral view (Fig. 21d); finely tuberculate (Fig. 21e) differentiating into a large rugulate marginal ridge (Figs 21c,g); sexine alveolate to columellate (Fig. 21j). Bladders three; hemispherical (Figs 21a,b) but sometimes compressed or laterally elongated; flaccid; clear outline; reticulum large meshed but often confused with heavy relief lines running from the point of attachment of the bladder to its periphery (Figs 21a,b); thickened internally; numerous micropunctae on outer surface (Fig. 21g). Sharp intersection of bladders and furrow but coarsely folded ventral roots of bladders tend to conceal the furrow rim (Fig. 21k); furrow triangular (Fig. 21h);

Figure 21. *Dacrycarpus dacrydioides.*

a - f Light micrographs (all x 990).
g - i Scanning electron micrographs.
j - l Transmission electron micrographs.

a. Polar view (distal).
b. Polar view (distal); large meshed bladder reticulum.
c. Polar view (proximal); distinct marginal ridge.
d. Lateral longitudinal view; lens shaped.
e. Polar view (proximal); tuberculate cap sculpturing.
f. Polar view (proximal); triradiate scar.
g. Lateral longitudinal view; marginal ridge (arrowed) (x 1400).
h. Polar view (distal); triangular furrow surrounded by three bladders (x 1350).
i. Furrow; rugulate sculpturing (x 4100).
j. Section through tectate cap (x 25000).
k. Section through junction of bladder and furrow. Sexine (S) separates from nexine (x 26000).
l. Section through rugulate furrow; sexine (arrowed), nexine (N), intine (I) (x 37000).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rugulate (Fig. 21i) with well developed nexine layer (Fig. 21 l).

Ueno (1957) and Cranwell (1961) report the presence of a triradiate scar in the middle of the body of the grain. Such a scar (or streak) marks the contact of the grains in the developing tetrad and is clearly illustrated by Bagnell (1975) for *Abies*. This study supports the findings of the previous workers with a very low frequency of seemingly aberrant grains observed (Fig. 21f) but cannot corroborate with Cranwell's (1940) description of 'broad slash like markings'. However, this does not discount the presence of them in other material.

Dacrycarpus dacrydioides falls into the same category as *Dacrydium cupressinum* in possessing markedly unique features (*viz.* the triangular furrow and three bladders) which separate it from other species no matter what orientation it displays in slide preparations. It is comparable only to *Pherosphaera* in the Podocarpaceae in possessing these features (Wodehouse 1935).

4.2.4 *Phyllocladus* L.C. and A. Richard

Phyllocladus is a genus of only six species native to Tasmania, New Zealand, the Philippines New Guinea and Borneo (Dallimore and Jackson 1966). The three species in New Zealand are endemic.

In *Phyllocladus* the photosynthetic organs are phylloclades and the ovules are partially enveloped by an 'aril'; these structures are not found in any other conifers (Sporne 1971). Couper (1953) observes that *Phyllocladus* pollen is distinctive generically but the three

Table 5. *Phyllocladus, Libocedrus* and *Agathis* pollen examined, geographical location, collector and herbarium reference.

TAXON	LOCALITY	COLLECTOR	HERBARIUM REFERENCE
Phyllocladus alpinus	Lake Haupari, Westland	D.M. Calder	CANU[1] 7334
	Ruapehu, Central North Island	M.S. McGlone	-
	Deep Creek, Okarito Road, Westland	I.R. Fryer	CHR[2] 179052
	Anti-crow Hut, Upper Waimakariri River, Canterbury	P. Wardle	CHR 185475
	Wilberforce River Valley, Canterbury	D.T. Pocknall	CANU 25245/49
Phyllocladus trichomanoides	Christchurch Botanic Gardens, Canterbury	B.P. Molloy	GEOG[3] 175
	Paihia, Northland	R.C. Lloyd	CANU 25242/44
	Mangukahia Valley, Whangarei, Northland	R. Cooper	CHR 207047
Phyllocladus glaucus	Waipoua, Northland	W. Silvester	CANU 9671
	Botanic Gardens, Wellington	A.L. Poole	CHR 69310
Libocedrus bidwillii	Scott's Track, Arthurs Pass, Canterbury	C.E. Foweraker	CANU 2095
	Christchurch Botanic Gardens, Canterbury	D.T. Pocknall	-
Libocedrus plumosa	Otari Gardens, Wellington	W.B. Bircher	-
Agathis australis	Christchurch Botanic Gardens, Canterbury	N.T. Moar	3787[4]
	Wiltons Bush, Wellington	N.M. Adams	2719[4]

[1] Department of Botany, University of Canterbury Herbarium

[2] Botany Division, D.S.I.R. Herbarium

[3] Department of Geography, University of Canterbury (Slide reference)

[4] Botany Division, D.S.I.R. (Slide reference)

Table 6. Summary of pollen measurements,[1] corpus shape and cap/surface sculpturing in *Phyllocladus*, *Libocedrus* and *Agathis*.

TAXON	TOTAL LENGTH		CORPUS BREADTH		BLADDER LENGTH		FURROW WIDTH		CORPUS SHAPE	DORSAL CAP SCULPTURE
	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE	SILICONE OIL	GLYCERINE		
Phyllocladus alpinus	32.81 ± 0.39 (30.6 - 35.7)	34.19 ± 0.49 (30.6 - 37.4)	25.67 ± 0.58 (20.4 - 30.6)	29.45 ± 0.38 (27.2 - 32.1)	8.75 ± 0.35 (6.8 - 11.9)	9.94 ± 0.28 (6.8 - 11.9)	12.92 ± 0.35 (10.2 - 15.3)	13.43 ± 0.24 (11.9 - 15.3)	Ellipsoidal	large tuberculate
Phyllocladus trichomanoides	32.64 ± 0.44 (28.9 - 35.7)	34.26 ± 0.47 (30.6 - 37.4)	17.60 ± 0.40 (13.6 - 20.4)	23.03 ± 0.53 (18.7 - 27.2)	8.41 ± 0.29 (6.8 - 10.2)	8.41 ± 0.31 (6.8 - 10.2)	11.39 ± 0.43 (8.35 - 13.6)	17.17 ± 0.44 (13.6 - 20.4)	Spheroidal or ellipsoidal	large tuberculate (reticulate)
Phyllocladus glaucus	20.46 ± 0.41 (17 - 23.8)	23.54 ± 0.51 (20.4 - 28.9)	17.85 ± 0.39 (15.3 - 20.4)	18.81 ± 0.47 (17 - 23.8)	4.72 ± 0.28 (3.4 - 6.8)	6.16 ± 0.27 (3.4 - 8.5)	11.13 ± 0.40 (8.5 - 13.6)	14.24 ± 0.19 (13.6 - 15.3)	Ellipsoidal	tuberculate-rugulate(?)
	DIAMETER								GRAIN SHAPE	
	SILICONE OIL	GLYCERINE								
Libocedrus bidwillii	25.16 ± 0.51 (20.4 - 27.2)	26.18 ± 0.38 (23.8 - 30.6)							Spheroidal	Granular with orbicules
Libocedrus plumosa	29.04 ± 0.55 (23.8 - 34)	30.09 ± 0.63 (23.8 - 35.7)							Spheroidal	Granular with orbicules
Agathis australis		52.71 ± 0.31 (46.9 - 58.4)							Spheroidal	Pitted

[1] Mean with standard error followed by range in parenthesis. All measurements in microns (μm).

New Zealand species have very similar pollen. The pollen has rudimentary bladders which Cranwell (1940) believes results in the inclusion of this genus in the Podocarpaceae.

Descriptions of Pollen

Phyllocladus alpinus Hook. f. (mountain tanekaha)
Figure 22a-n.

Cap ellipsoidal; large tuberculate over much of cap (Figs 22b,e,g); small tuberculate (tectate-perforate) region of 'weakness' at lateral margins (Figs 22d,k,m); tuberculae spinose (Fig. 22k); sexine granular to alveolate (Fig. 22 l). Bladders small, rudimentary (Figs 22a,h); usually entire but sometimes consist of 1-4 distinct folds (Figs 22c,f); barely project beyond the corpus; sparse reticulum (Fig. 22a); micropunctae and spinose bladder surface (Fig. 22j). Sharp intersection of bladder and furrow with prominent furrow rim (Figs 22a,h,i); furrow wide and smooth (Figs 22i,n).

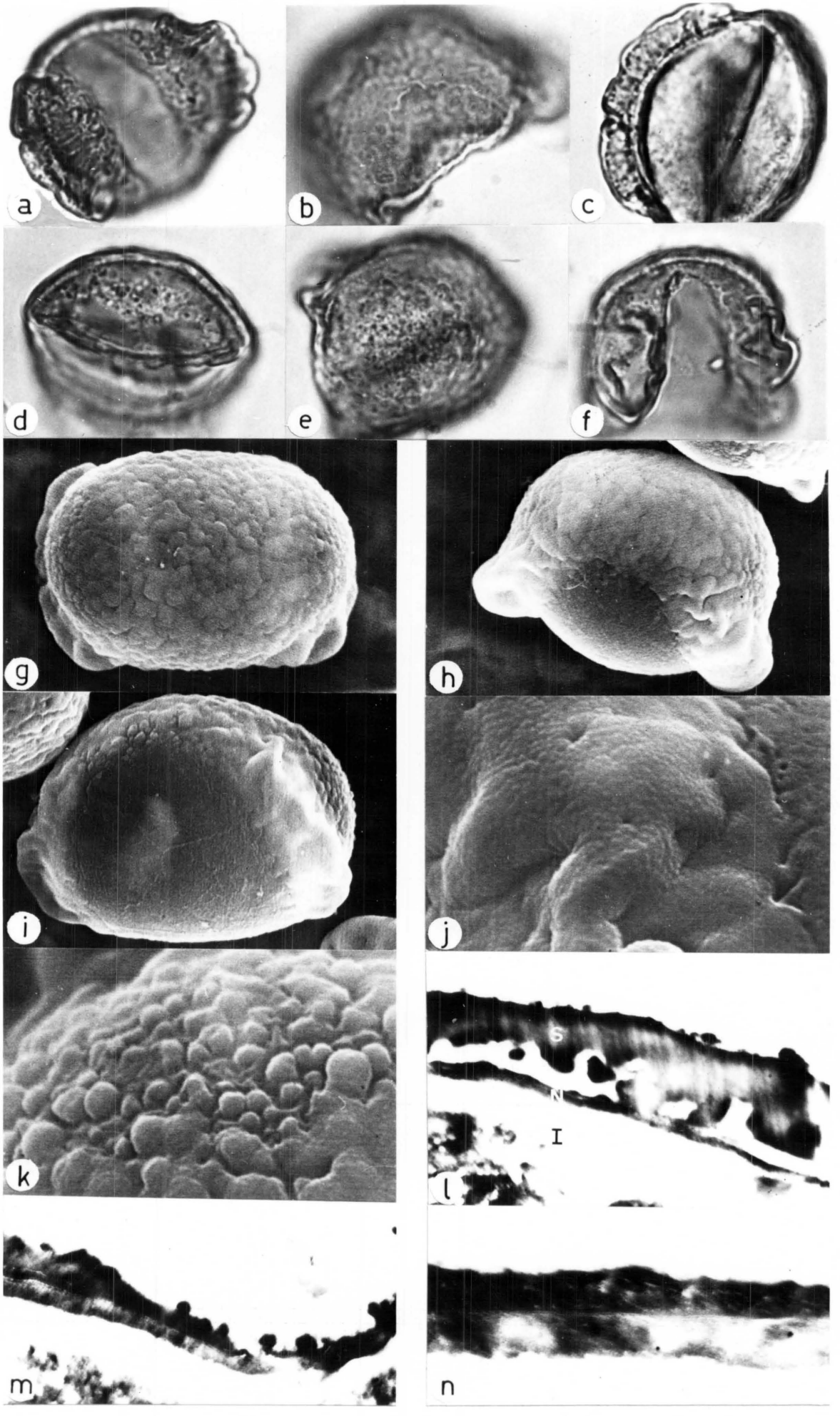
Pollen of *Phyllocladus* is well preserved in peats and is probably that of *P. alpinus* as it is the most widespread of the three species based on present day distribution, at least. Certainly, the presence of *Phyllocladus* with *Coprosma* and *Myrsine* shrubland at Cass (Moar 1971; Lintott and Burrows 1973) would be linked with *P. alpinus* on present day ecologic interpretations.

Specific identification probably lies in the morphology of the cap as a difference is noted in this study with modern material. Another possibility is the use of macrofossils. The phylloclades of *P. alpinus* are clearly distinct from the other species which in turn differ from

Figure 22. *Phyllocladus alpinus.*

a - f Light micrographs (all x 1300).
g - k Scanning electron micrographs.
l - n Transmission electron micrographs.

a. Polar view (distal); flattened bladders and narrow furrow.
b. Lateral longitudinal view; tuberculate cap sculpturing.
c. Lateral longitudinal view; clear bladder outline.
d. Lateral longitudinal view; small tuberculate region of 'weakness'.
e. Polar view (proximal); tuberculate cap sculpturing.
f. Polar view (distal).
g. Polar view (proximal); ellipsoidal cap with large tuberculate sculpturing (x 1750).
h. Lateral longitudinal view, sharp distinction between cap and furrow. Bladders small (x 1750).
i. Polar view (distal); wide, smooth furrow (x 9000).
j. Spinose bladder surface with micropunctae (x 9000).
k. Small tuberculate region of 'weakness' (x 9000).
l. Section through alveolate sexine (S), nexine (N) and intine (I) of cap (x 17000).
m. Section through tectate-perforate region of 'weakness' (x 21000).
n. Section through furrow (x 38000).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each other in seed presentation (Allan 1961).

Phyllocladus trichomanoides D. Don (tanekaha) Figure 23a-l. Cap spheroidal to ellipsoidal; large tuberculate (Figs 23f,h); small tuberculate (tectate-perforate) region of 'weakness' at lateral margins (Figs 23g,h,l); sexine mostly granular in middle of cap (Fig. 23i). Bladders much as in *P. alpinus* except for more folds near the lateral roots (Figs 23a,b,c,d,g); sexine layer thick and rigid with few infratectal sexinous elements (Fig. 23j). Furrow rim (Figs 23b,g); furrow as in *P. alpinus* (Figs 23g,k).

There are three features in which *P. trichomanoides* differs from *P. alpinus*:

(i) more folded bladders (especially near the lateral roots);

(ii) larger sculpturing of the cap. Large tuberculae protrude more than in *P. alpinus*;

(iii) grain more spheroidal.

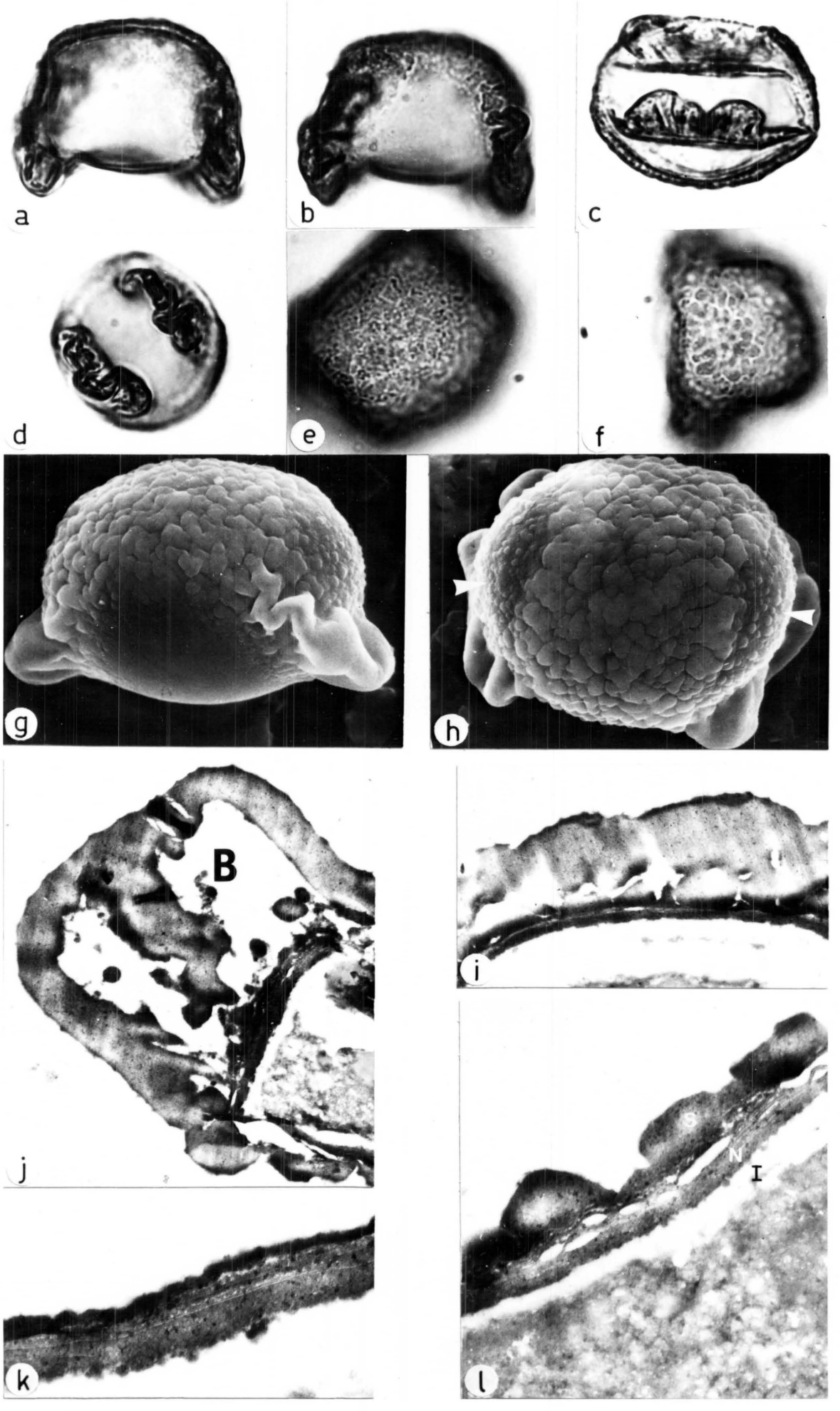
All three features are clearly evident in the scanning electron microscope but the small grains in *Phyllocladus* make specific identifications under the light microscope very difficult.

Phyllocladus glaucus Carr. (toatoa) Figure 24a-l. Cap ellipsoidal; much smaller in total length (20 µm) than *P. alpinus* and *P. trichomanoides* (both 32 µm); tuberculate-rugulate (Figs 24g,j) but granular under light microscope (Fig. 24d); region of 'weakness' (Figs 24g,h); elongate rugulae common, traversing the cap from bladder to bladder (Fig. 24g) suggesting a marginal ridge; sexine alveolate

Figure 23. *Phyllocladus trichomanoides.*

a - f Light micrographs (all x 1300).
g - h Scanning electron micrographs.
i - l Transmission electron micrographs.

a. Lateral longitudinal view, cross section.
b. Lateral longitudinal view; sharp distinction between cap and furrow.
c. Polar view (distal).
d. Polar view (distal); folded bladders.
e. Polar view (proximal).
f. Polar view (proximal); large tuberculate cap sculpturing.
g. Lateral longitudinal view; folded bladders and smooth furrow (x 2000).
h. Polar view (proximal); regions of 'weakness' (arrowed) and tuberculate cap sculpturing (x 2000).
i. Section through cap (x 16000).
j. Section through bladder (B) showing sexine separated from the nexine (x 12000).
k. Section through furrow (x 38000).
l. Section through region of 'weakness'; tuberculate sexine (S), nexine (N) and intine (I) (x 28000).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(Fig. 24k). Bladders exceedingly small, at least half the size of those in *P. alpinus* and *P. trichomanoides*; appear as irregular rigid folds running across the grain (Figs 24c,e,f). Furrow finely rugulate (Fig. 24i), with thin sexine overlying wide laminated nexine (Fig. 24 l).

The pollen of *P. glaucus* probably occurs freely in peat. Its present limited distribution may reflect climatic tolerances which would be important in assessing vegetation history and climate but its propensity to cross with *P. trichomanoides* tends to limit its benefit for ecological interpretation. Grain size makes specific identification difficult because the fine features (cap sculpture and bladder furrow junction) are those which are considered diagnostic. Small bladders and overall smallness are perhaps the best characteristics to use for this species.

The pollen of *Phyllocladus* shows a basic uniformity which poses severe identification problems for a pollen analyst. The scanning electron microscope is important in the delineation of the three species but the diagnostic features are often obscured and not seen in the light microscope.

4.3 CUPRESSACEAE

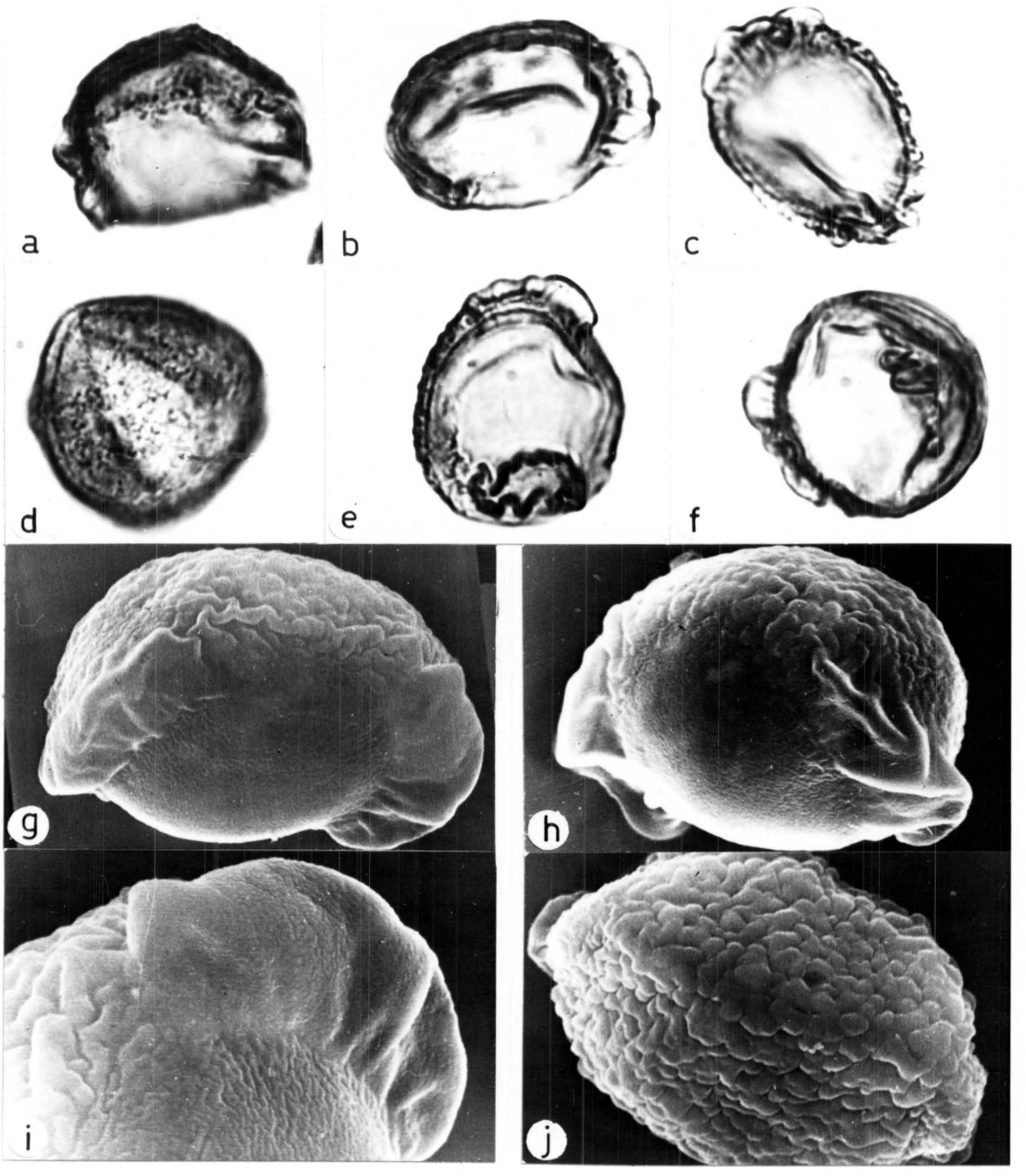
4.3.1 *Libocedrus* Endlicher pro parte

Libocedrus is the only representative of the Cupressaceae in New Zealand. There are five species, two in New Zealand and three in New Caledonia. The pollen of the New Zealand species, *L. bidwillii* and *L. plumosa*, have been described by Cranwell (1940); they are very similar and are

Figure 24. *Phyllocladus glaucus.*

a - f Light micrographs (all x 1300).
g - j Scanning electron micrographs.
k - l Transmission electron micrographs.

a. Lateral longitudinal view.
b. Polar view (distal).
c. Polar view (distal); small bladders and wide furrow.
d. Polar view (proximal); granular surface ornamentation.
e,f. Polar view (distal); folded bladders.
g. Lateral longitudinal view; elongate rugula on cap, region of 'weakness' (x 2000).
h. Ventro-lateral view; folded bladders (x 2000).
i. Spinose bladder surface. Finely rugulate furrow (x 6700).
j. Polar view (proximal); tuberculate cap sculpturing (x 2500).
k. Section through tectate cap. Alveolate sexine (S) partially separated from nexine (N) and intine (I) (x 31000).
l. Section through furrow (x 34000).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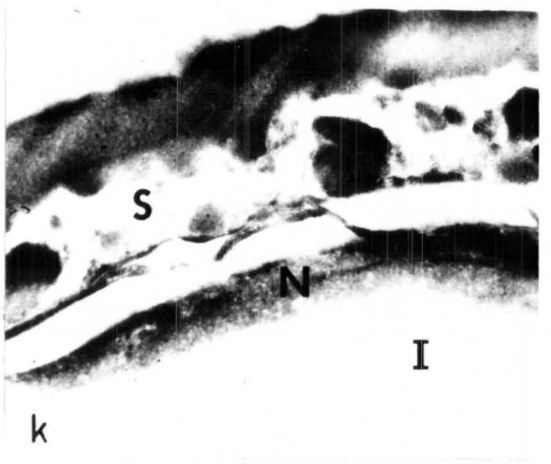
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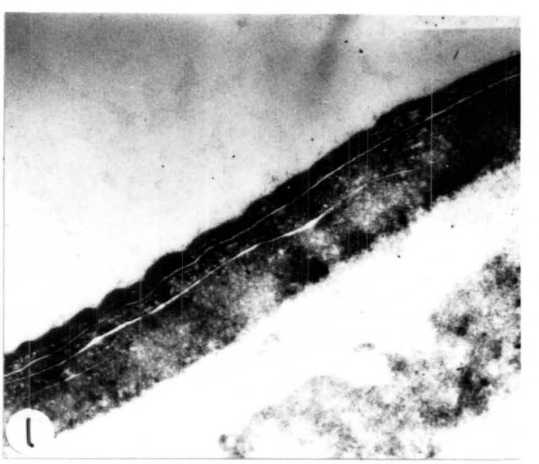
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without bladders.

Descriptions of Pollen

Libocedrus plumosa (D. Don) (kawaka) Figure 25a-m. Apolar; grain spheroidal, small (diameter 24-34 µm in silicone oil), commonly collapsed; sexine tectate-perforate (Figs 25 l,m) consisting of star-shaped orbicules (Figs 25c,d,e,g,h,k); nexine comprises white line lamellations (Fig. 25m), appearing finely granular with light microscope (Figs 25a,b); pseudopore marked by a papilla (Figs 25i,j); intine thickened representing up to half the volume of the grain in fresh state.

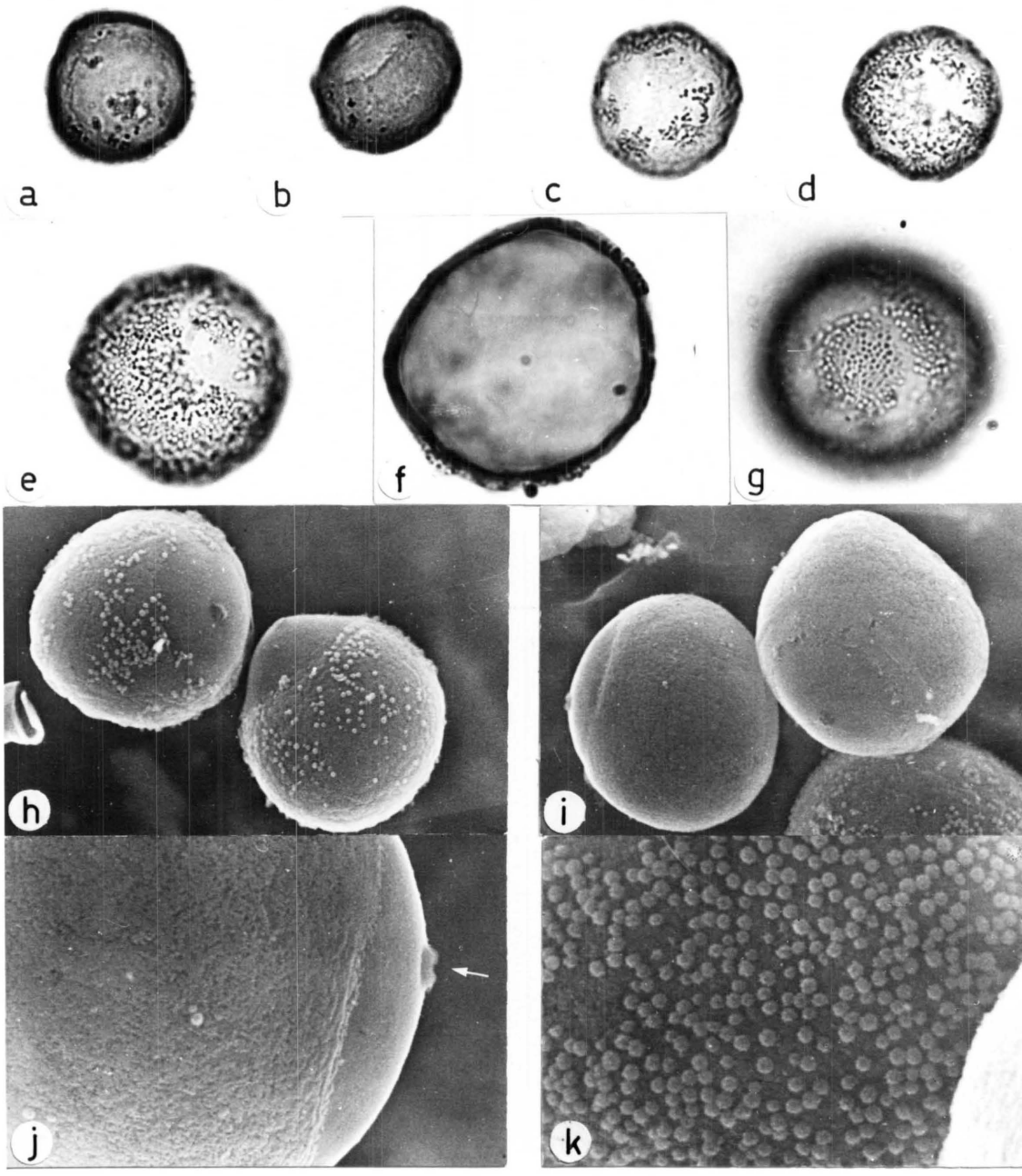
Libocedrus bidwillii Hook. f. (kaikawaka) Figure 26a-m. Apolar; grain spheroidal and smaller than *L. plumosa* (diameter 20-27 µm in silicone oil); in all other features it resembles those displayed in *L. plumosa*.

Ueno (1959) refers to a primitive germ pore in all genera of the Cupressaceae. He specifically studied *Libocedrus decurrens* and his work is supported by the present observations with the pollen of *L. bidwillii* and *L. plumosa*. These observations refute the description of Wodehouse (1935) and Cranwell (1940) who suggest the absence of a pore or furrow in *Libocedrus* pollen. The pore, however, appears to be functionless and the thick 'intine' behaves as a furrow, swelling when wet and casting off the exine before emergence of the germ tube. Wetting and germination tests on *L. bidwillii* pollen confirm this theory on pollen tube germination (refer Fig. 26h). Ho and Sziklai (1973) suggest that the papilla functions as a germinal pore. Further

Figure 25. *Libocedrus plumosa.*

a - g Light micrographs (all x 620 except as otherwise stated).
h - k Scanning electron micrographs.
l - m Transmission electron micrographs.

a. Equatorial view.
b. Polar view; pseudopore.
c. Equatorial view.
d. Equatorial view.
e. Equatorial view; orbicular surface sculpturing (x 880).
f. Equatorial view; cross section (x 1150).
g. Equatorial view (x 880).
h. Two grains; orbicular surface sculpturing and pseudopores (x 900).
i. Two grains; pseudopores (x 950).
j. Equatorial view; pseudopore with papilla (arrowed) (x 3800).
k. Surface sculpturing (x 5600).
l. Section through tectate-perforate exine (x 33000).
m. Section through orbicule (O), laminated nexine (N) and wide intine (I) (x 42000).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experiments may confirm this. The thick intine is therefore not preserved and the pollen of *Libocedrus* as in other Cupressaceae, is represented in the fossilised condition by the discarded exinous case.

Because there is little variation between the pollen of *L. plumosa* and *L. bidwillii* specific identification is impossible. This is unfortunate from a pollen analytical point of view because the two species have vastly different ecological amplitudes and are recorded in high frequencies (>40%) in some peats (McGlone and Topping 1977; McGlone unpublished - Ahukawakawa swamp, Mt Egmont). Knowledge of the origins of the other pollen in such samples may help in making intuitive assumptions of the affinity of *Libocedrus* pollen. Couper (1951) remarks that *Libocedrus* pollen is very delicate, but its under-representation in our fossil floral record is either more likely to have resulted from its confusion with other pollen types or it being frequently overlooked because of its collapsed and distorted condition, than to being destroyed.

4.4 ARAUCARIACEAE

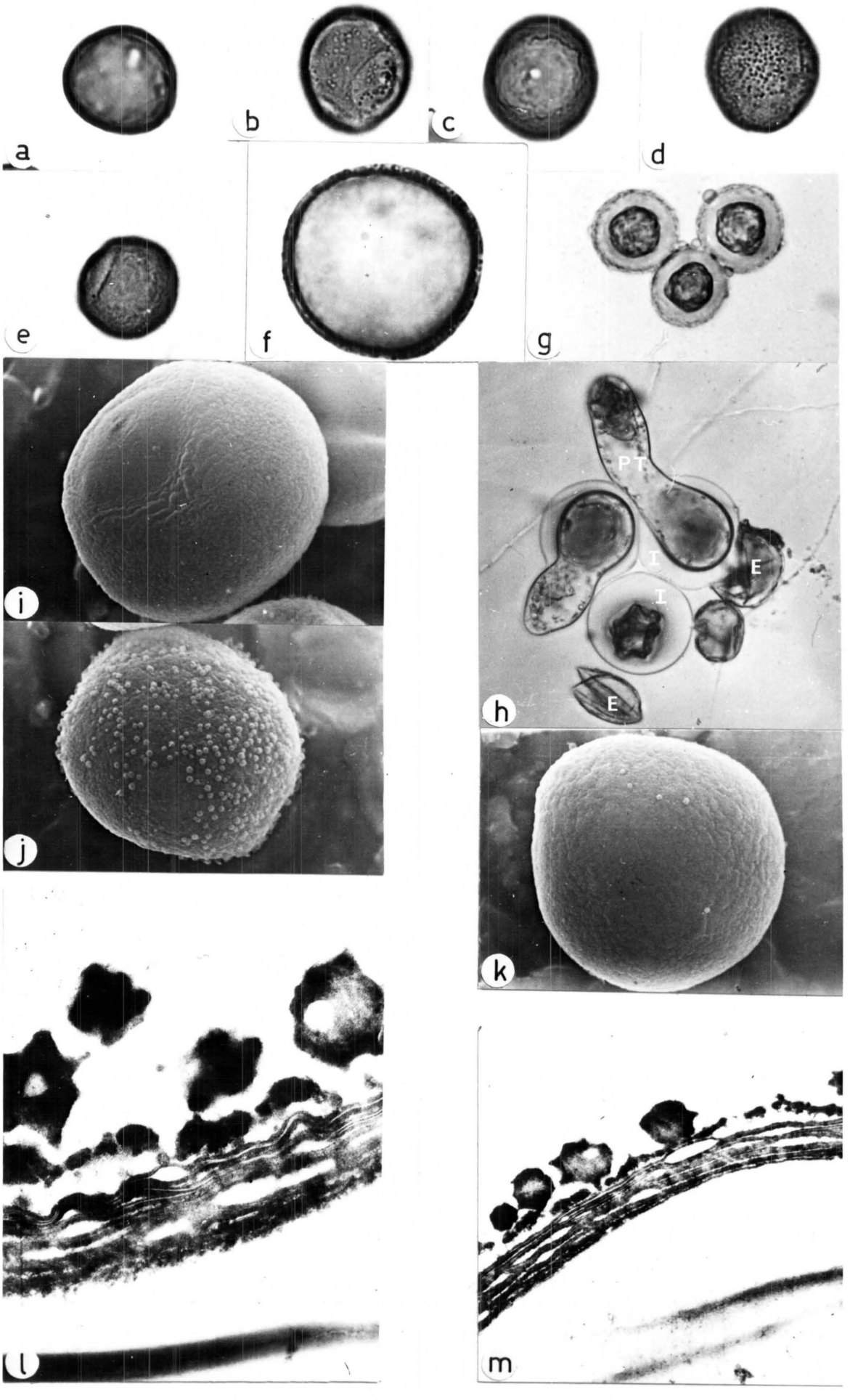
4.4.1 *Agathis* Salisbury

Agathis is a genus of twenty species and is exclusively eastern, extending from the Philippines through New Caledonia and Australia to New Zealand and from Malaya to Fiji. The only representative in New Zealand is *Agathis australis*. The pollen is wingless and Wodehouse (1935) believes it to represent the complete obliteration of furrow and pore as it lacks a furrow rim.

Figure 26. *Libocedrus bidwillii.*

a - h Light micrographs (all x 620 except as otherwise stated).
i - k Scanning electron micrographs (all x 2000).
l - m Transmission electron micrographs.

a. Equatorial view; cross section.
b. Equatorial view.
c. Polar view; pseudopore.
d. Equatorial view; orbicular surface sculpturing.
e. Equatorial view.
f. Equatorial view; cross section (x 1150).
g. Fresh pollen prior to wetting.
h. After three days; intine (I) swollen, exine (E) cast and pollen tube (PT) has emerged.
i. Polar view; pseudopore with papilla.
j. Equatorial view; orbicular surface sculpturing.
k. Equatorial view.
l,m. Sections through tectate-perforate exine (l x 42000, m x 33000).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Description of Pollen

Agathis australis Salisb. (kauri) Figure 27a-h.
Apolar; grain spheroidal, sometimes ellipsoidal; outer surface delicately and evenly pitted (Figs 27a,d,e); some grains have 1-3 germinal furrows or ectocolpi (Figs 27f,g,h).

The description of *A. australis* pollen is based on Cranwell (1940) and reference slides held at the Botany Division, Department of Scientific and Industrial Research, Lincoln. This was necessary because all fresh and herbarium collected male cones were devoid of pollen. The pollen seems to mature in a short time and is disseminated almost immediately. Consequently it was not possible to examine *A. australis* pollen with the scanning and transmission electron microscopes.

Because *Agathis* is monotypic in New Zealand there is no difficulty in pollen identification among the gymnosperms in recent times. Evans (1937) suggests its history in Tertiary times is obscured by the probable presence of other members of the Araucariaceae about that time. Cranwell (1940) points out that pollen of *A. australis* bears a superficial resemblance to pollen of *Hypolaena (Calorophus, Empodisma)* and N.T. Moar (pers. comm.) reports misidentifications in past work. In current research in the Bay of Plenty, North Island, M.S. McGlone (pers. comm.) has frequently recorded *A. australis* pollen.

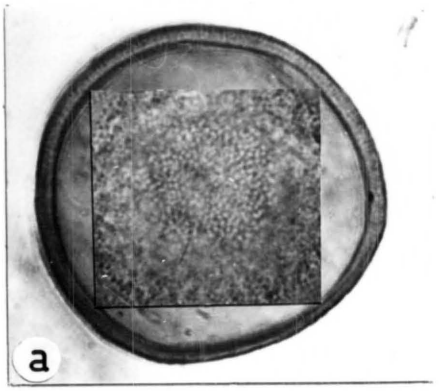
4.5 KEY TO THE POLLEN GRAINS OF THE NEW ZEALAND GYMNOSPERMS

The following key does not consider any abnormalities in pollen brought about in their development and is based

Figure 27. *Agathis australis*.

a - h Light micrographs (all x 700).

a. Equatorial view; cross section.
b. Polar view; cross section.
c. Equatorial view.
d. Equatorial view.
e. Equatorial view.
f. Equatorial view; ectocolpus.
g. Polar view; pitted surface sculpturing.
h. Polar view; ectocolpi.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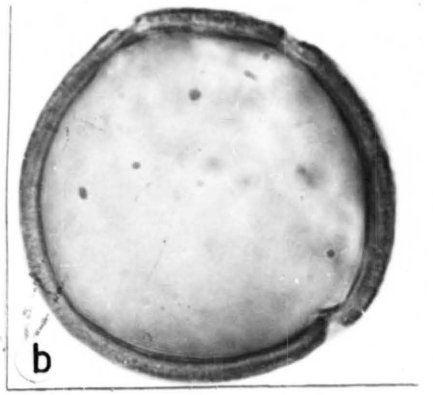
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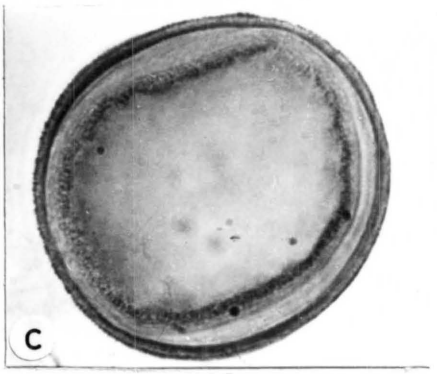
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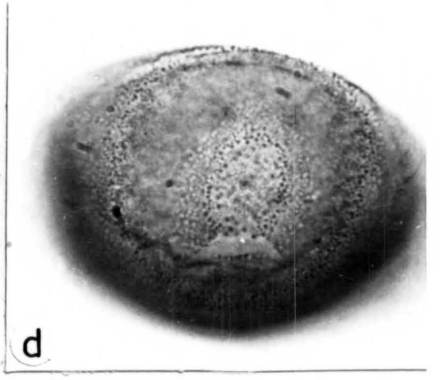
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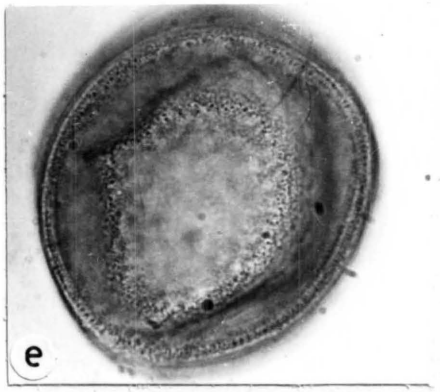
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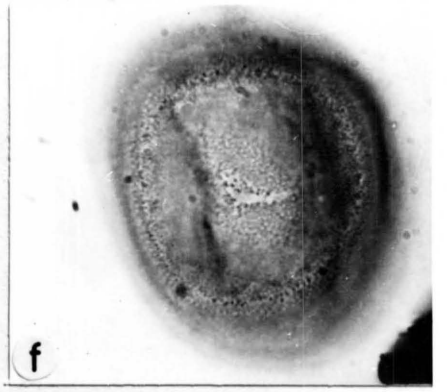
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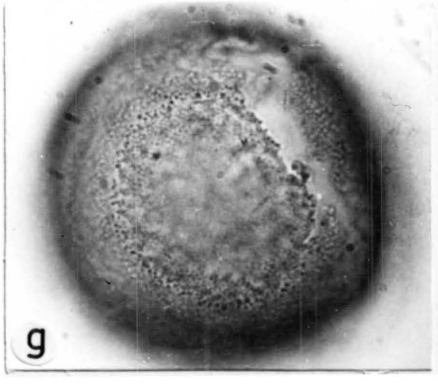
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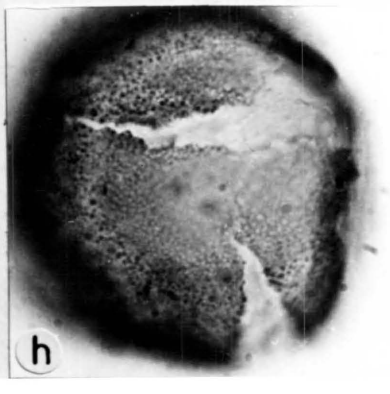
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entirely on observations of fresh (modern) material. Therefore, it cannot allow for any changes incurred during fossilisation and preservation of pollen in past times.

1. With bladders . . . . . 2.
   Without bladders . . . . . 3.

2. Two bladders . . . . . 4.
   Three bladders . . . . . *Dacrycarpus dacrydioides*

3. With germinal furrows and pitted exine sculpturing . . . . . *Agathis australis*
   With pseudopores and orbicules on outer surface . . . . . *Libocedrus plumosa*
   L. bidwillii

4. Bladders with radial thickenings . . . . . 5.
   Bladders with reticulate thickenings . . . . . 6.
   Bladders small, folded; rudimentary . . . *Phyllocladus alpinus*
   P. trichomanoides
   P. glaucus

5. Bladders with coarse tuberculate-rugulate sculpturing over entire grain; rudimentary . . . . . *Dacrydium cupressinum*
   Bladders large, clearly defined; tuberculate sculpturing over cap of grain . . . . . 7.

6. Exine of cap coarsely rugulate with small spinules predominating on surface of cap and bladders . . . . . 8.
   Exine of cap weakly sculptured, mostly tuberculate . . . . . 9.

7. Grain small (<45 µm overall length) . . . *Dacrydium kirkii*
   Grain large (>50 µm overall length) . . . *D. bidwillii*
   D. biforme

8. Bladders with numerous heavy relief lines; well defined reticulum . . . . . 10.
   Bladder reticulum sparse but well defined . . . . . *Podocarpus acutifolius*
   P. totara var. *waihoensis*

Bladder reticulum diffuse;
delicately meshed . . . . . *P. nivalis*

9. Bladders small, with regular polygonal or elongated meshes; fine, delicate 'cauliflower-type' protrusions over cap of grain . . . . . *Dacrydium colensoi*

Bladders large with numerous folds; irregularly distributed elongated meshes . . . . . *D. laxifolium*

Bladders large meshed with blindly branched system; overall length of grain >65 µm . . . . . *Podocarpus ferrugineus*

Bladders small meshed . . . . . 11.

10. Cap sculpture irregular; grain often ellipsoidal . . . . . *P. totara*

Cap sculpture regular; grain spheroidal . . . . . *P. hallii*

11. Bladder meshes complete polygons; overall length of grain <60 µm . . . . *P. spicatus*

Bladder meshes irregular; cap almost sculptureless with distinct regions of 'weakness'; wide furrow . . . . . *Dacrydium intermedium*

CHAPTER 5

RELATIVE POLLEN REPRESENTATION IN RELATION TO VEGETATION COMPOSITION, SOUTH WESTLAND*

5.1 INTRODUCTION

Many of the studies mentioned in Chapter 2 have compared the pollen rain to qualitative descriptions of the local and regional vegetation. A more meaningful technique is to compare the pollen rain to a quantitative assessment of the vegetation. Such parameters as basal area (Davis and Goodlett 1960; Potter and Rowley 1960; Anderson 1967), tree composition (Bent and Wright 1963; Dąbrowski 1975) and cover values (Hartman 1968; Birks 1977) have been employed to give a quantitative correlation between modern pollen rain and species abundance in the vegetation. This allows determination of the ratio between the percentage of each taxon in the pollen rain and the percentage of the same taxon in the vegetation (Livingstone 1968), resulting in a correction factor or R-value. Tsukada (1958 - in Davis 1963) proposed correction factors for Japanese pollen diagrams. The R-value for a species 'a' is calculated thus:

$$R(a) = \frac{\text{species 'a' pollen percentage}}{\text{species 'a' vegetational percentage}}$$

The terms over-representation and under-representation depend on whether the R-value is larger or smaller than 1 (Flenley 1973; Dodson 1975). Davis (1963) showed that the

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*An abridged version of this work has appeared in *New Zealand Journal of Botany* 16: 379-86 (1978).

R-value for a species would vary from case to case depending on the relative importance of heavy and light pollen producing species in the vegetation, but the ratios of the R-values for the various taxa to each other would be constant. There are shortcomings in their use (Faegri 1966), and difficulties inherent in the use of R-values include the definition of a measure or the 'quantity of vegetation' and the 'catchment' area for influx of pollen (Caseldine and Gordon 1978). Janssen (1967) has stressed that R-values change from one vegetation type to another due to variations in the pattern of vegetation. He subsequently suggested (Janssen 1970) that auxillary diagrams eliminating pollen types that are grossly over-represented in one way or another may be more useful.

5.2 STUDY METHODS

The data presented here comes from moss cushions collected at six localities in the vicinity of Harihari, South Westland. The pollen rain is related to a quantitative description of the vegetation types from which the samples were taken. Appendix IIIa records the overall results of the vegetation survey carried out in conjunction with the modern pollen rain analysis, and full species lists for each site.

Some problems of interpretation remain with respect to the pollen rain because the surrounding vegetation also contributes pollen. This problem is frequently encountered by workers comparing surface pollen spectra with present vegetation (Lichti-Federovich and Ritchie 1968).

The R-values of some key phytosociological plant taxa

are calculated, using basal area as a forest parameter, and considered in this chapter. Variations of the nature pointed out by other authors will be discussed and in the light of these their value to New Zealand pollen studies will be assessed.

5.3 THE VEGETATION OF THE HARIHARI AREA

Before clearance the seaward morainic slopes and terraces in the Harihari region of South Westland supported a mosaic of podocarp and hardwood forests (Godley 1976). *Dacrydium cupressinum* dominates except in isolated areas of special character such as wet swampy localities where *Dacrycarpus dacrydioides* prevails, natural basins at low altitudes where *Dacrydium colensoi* forms bog forests, and areas of recent alluvium where *Podocarpus spicatus* and *P. totara* var. *waihoensis* dominate (Holloway 1954a). *Podocarpus ferrugineus* is commonly associated with *D. cupressinum* and on steeper slopes (e.g. Poerua State Forest east of the Harihari settlement) may attain comparable densities. *Weinmannia racemosa* and *Quintinia acutifolia* form an important component of these vegetation complexes and in some instances may be numerically dominant. Most of the cleared land (i.e. river flats) is used for dairy farming. In addition, the understorey of some forests show evidence of grazing by cattle and of logging by the New Zealand Forest Service. Because much of the original vegetation has been destroyed or altered in structure some of the conclusions reached in this study may not be directly applicable to Quaternay vegetation history. Figure 28 outlines the broad vegetation patterns.

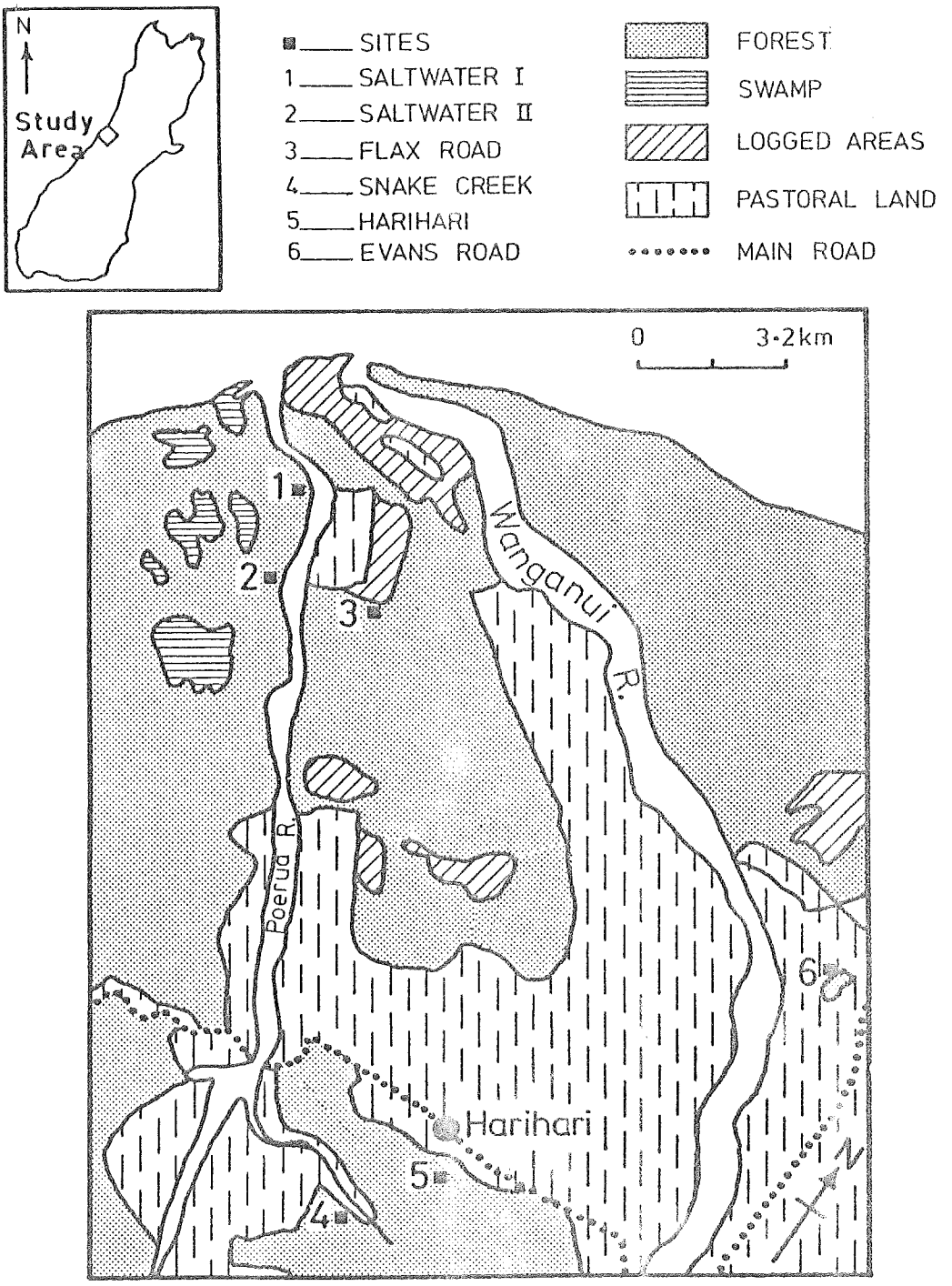


Figure 28. Location of sites in the Harihari region, South Westland. Inset: South Island; showing study area.

5.4 VEGETATION AND POLLEN RAIN AT EACH SAMPLING SITE

Figure 28 shows the locations of six sampling sites. At each site several moss cushions were collected and the individual sample data are presented in Figure 33. These figures are percentage calculations based on a sum of total pollen and spores. Figure 34 compares the basal area data and pollen frequencies for the major tree taxa. The pollen figure is the mean of all surface samples at each site and in some cases the standard error (SE) is included on the diagram. A summary of the data plotted in Figure 34 and SE's are included in Table 7 which also indicates the R-values calculated for each taxa.

In the following discussion the values in parentheses represent percentages of total basal area of plants 1.5 m tall and those in square brackets the percentage of total pollen and spores averaged over the sub-samples of each site. The results have been interpreted in relation to the vegetation as follows:

i. over-represented: where pollen percentage is greater than percentage of source taxa within the vegetation.

ii. well-represented (or proportionately represented): where pollen percentage approximates source taxa percentage in the vegetation.

iii. under-represented: where pollen percentage was zero or smaller than source taxa percentage in the vegetation (after Dodson 1976).

Table 7. Total basal area, pollen representation and R-values for tree types, Harihari, South Westland.
(Pollen sum = total pollen + spores)

TAXON	SALTWATER I			SALTWATER II			FLAX ROAD			SNAKE CREEK			HARIHARI			EVANS ROAD		
	Basal Area %	Pollen %	R-value	Basal Area %	Pollen %	R-value	Basal Area %	Pollen %	R-value	Basal Area %	Pollen %	R-value	Basal Area %	Pollen %	R-value	Basal Area %	Pollen %	R-value
Dacrycarpus dacrydioides	80.12	38.4 (±5.93)	0.5	61.7	6.4 (±1.31)	0.1	-	2.7 (±0.36)	-	3.5	2.7 (±0.56)	0.8	-	0.3	-	51.7	14.4 (±5.05)	0.3
Dacrydium cupressinum	-	2.4	-	-	0.9	-	62.5	42.2 (±2.90)	0.7	11.6	22.1 (±7.41)	1.9	18.8	13.2 (±2.0)	0.7	-	2.4 (±1.24)	-
D. colensoi	-	0.6	-	-	0.5	-	-	2.1	-	4.3	0.1	0.02	-	0.1	-	-	1.3	-
Phyllocladus alpinus	-	0.4	-	-	0.6	-	1.9	5.7 (±0.25)	3.0	-	0.7	-	-	0.7	-	-	0.4	-
Podocarpus ferrugineus	-	1.8	-	9.4	0.3	0.03	-	3.4 (±0.99)	-	-	1.8	-	24.8	13.7 (±1.31)	0.6	-	1.4	-
P. spicatus	-	-	-	8.1	1.3	0.2	-	0.1	-	-	0.4	-	-	0.8	-	-	-	-
Ascarina lucida	-	0.1	-	-	-	-	-	0.6	-	-	0.4	-	1.2	3.8 (±0.37)	3.2	-	0.3	-
Carpodetus serratus	0.4	0.2	0.5	3.4	0.09	0.03	-	0.03	-	1.5	0.1	0.07	-	0.3	-	-	0.1	-
Coprosma	0.1	5.2 (±1.0)	52	0.7	1.7	2.4	0.02	4.2 (±0.45)	210	0.4	3.0 (±0.48)	7.5	-	1.3	-	0.7	4.9 (±1.41)	7.0
Elaeocarpus	-	0.4	-	-	1.0	-	-	1.1	-	-	0.7	-	5.5	0.1	0.02	-	6.2 (±4.78)	-
Griselinia littoralis	0.6	1.2	2.0	-	0.6	-	-	0.5	-	6.0	2.2	0.4	-	0.7	-	-	0.6	-
Leptospermum scoparium	-	0.9	-	-	-	-	-	0.2	-	-	0.1	-	-	0.1	-	30.3	22.9 (±7.13)	0.8
Pennantia corymbosa	0.1	0.1	1.0	2.7	14.7 (±5.62)	5.4	-	-	-	1.1	1.0	0.9	-	0.1	-	-	1.3	
Pseudopanax	1.3	0.8	0.6	-	0.7	-	1.4	0.3	0.2	1.6	0.5	0.3	-	0.4	-	10.5	1.7	0.2
Quintinia acutifolia	-	1.2	-	-	3.1 (±1.21)	-	5.3	2.8 (±0.41)	0.5	-	1.4	-	8.1	9.2 (±1.20)	1.1	-	1.0	-
Weinmannia racemosa	10.1	5.6 (±1.58)	0.5	-	3.8 (±1.83)	-	24.8	7.3 (±1.47)	0.3	54.5	23.2 (±4.55)	0.4	41.4	5.3 (±0.84)	0.1	-	4.7 (±1.29)	-
Cyathea smithii	3.5	2.1	0.6	12.5	36.9 (±10.19)	3.0	-	3.8 (±0.31)	-	6.4	17.2 (±2.29)	2.7	-	13.7 (±1.88)	-	-	0.9	-
Dicksonia squarrosa	3.8	5.5 (±1.02)	1.4	1.1	1.7	1.5	3.6	0.7	0.2	4.9	3.4 (±1.13)	0.7	-	1.8	-	-	0.2	-

[a] Mean pollen percentages often followed by standard error (SE) in parentheses.

Figure 29. Forest of *Dacrycarpus dacrydioides*, *Podocarpus spicatus* and *P. ferrugineus* at the site of Saltwater II.

Figure 30. *Dacrydium cupressinum* dominated forest at Flax Road.

5.4.1 Saltwater I (NZMS 1 S63 043134, Figure 28)

6 samples: SI-A, SI-B, SI-C, SI-D, SI-E, SI-F

The forest at this site is an almost pure stand of *Dacrycarpus dacrydioides* (80) in a swampy locality on the southern bank of the Poerua River. It is one of the few remnants of its type left in Westland. Under the dense *Dacrycarpus* canopy exist scattered individuals of *Weinmannia racemosa* (10), *Carpodetus serratus* (1), *Pseudopanax crassifolius* (1), *Dicksonia squarrosa* (4) and *Cyathea smithii* (3.5). There is a dense ground cover of *Metrosideros perforata*, *Nertera dichondraefolia*, *Asplenium bulbiferum* and *Hymenophyllum* spp.

Dacrycarpus dacrydioides is under-represented [38] despite dominating the pollen spectrum. This is best explained by the presence at the sampling site of *Coprosma*, *Weinmannia* and *Dicksonia squarrosa*. These plants contribute, in this case, little to the basal area but still shed pollen or spores close to the source trees. It is difficult to assess the representation of *Phymatosorus* spores as two of the six sub-samples were collected near *Phymatosorus* plants.

5.4.2 Saltwater II (NZMS 1 S63 053110, Figures 28 and 29)

4 samples: SII-A, SII-B, SII-C, SII-D

The canopy is dominated by *Dacrycarpus dacrydioides* (62) but scattered individuals of *Podocarpus ferrugineus* (9) and *P. spicatus* (8) are present. The canopy is more open than at Saltwater I and below there is a sparse understorey consisting mainly of *Pennantia corymbosa* (2), *Carpodetus serratus* (3), *Pseudowintera colorata* (1), *Coprosma rotundifolia* (1) and *Cyathea smithii* (12.5). *Uncinia* spp. and *Metrosideros perforata*

Figure 31. A clearing in the podocarp/hardwood forest at Harihari. The ground is covered by *Blechnum* species, *Metrosideros perforata*, *M. diffusa* and podocarp regeneration.

Figure 32. *Leptospermum scoparium* and *Dacrycarpus dacrydioides* at Evans Road.

form most of the sparse ground cover.

An exceedingly low pollen frequency for *Dacrycarpus* [6] provides a striking example of the under-representation of this species. The presence of *Cyathea smithii*, a tree fern regularly over-represented in forest pollen spectra and *Pennantia corymbosa* at the site of deposition tend to conceal the *Dacrycarpus* pollen recorded in the samples. Both of these species are seen to have poor relative export (Chapter 2, p. 14); this is evident from large standard errors calculated on the overall mean. *Coprosma*, *Griselinia* and *Dicksonia squarrosa* are more or less proportionately represented while *Podocarpus ferrugineus*, *P. spicatus* and *Carpodetus serratus* are under-represented. A surprising feature of the pollen spectrum is the low frequency of *Dacrydium cupressinum* [1] not present in the immediate sample area but forming extensive pole stands 100 m to the south. Pollen of *Quintinia* [4] is derived from a distant source.

5.4.3 Flax Road (NZMS 1 S63 075114, Figures 28 and 30)

6 samples: FLAX.A, FLAX.B, FLAX.C, FLAX.D, FLAX.E, FLAX.F

Milling operations in the 1940's (P. Mawson, pers. comm.) removed all of the *Podocarpus ferrugineus* and many of the larger *Dacrydium cupressinum* trees from the Flax Road site. Nevertheless *D. cupressinum* remains dominant in terms of basal area (63). As a consequence of the logging *Phyllocladus alpinus* (2), *Weinmannia racemosa* (25) and *Quintinia acutifolia* (5) have become abundant in the understorey. The ground cover is limited mainly to *Sphagnum* moss due to poor drainage and past disturbances.

Pollen of *Dacrydium cupressinum* [42] is well represented and dominates the pollen spectrum. Irregularity of *D. cupressinum* flowering in the years since logging and the presence of the locally over-represented genera *Phyllocladus* and *Cyathea* may account for the disparity between the basal area and pollen percentages. The pollen frequency for *Podocarpus ferrugineus* [4] probably results from its occurrence prior to logging. The open nature of the site has resulted in minimal sampling variability (see Table 7 and Figure 33) from one sample to another and seemingly provides an adequate record of the local vegetation.

5.4.4 Snake Creek (NZMS 1 S64 138973, Figure 28)

6 samples: SNAK.A, SNAK.B, SNAK.C, SNAK.D, SNAK.E, SNAK.F

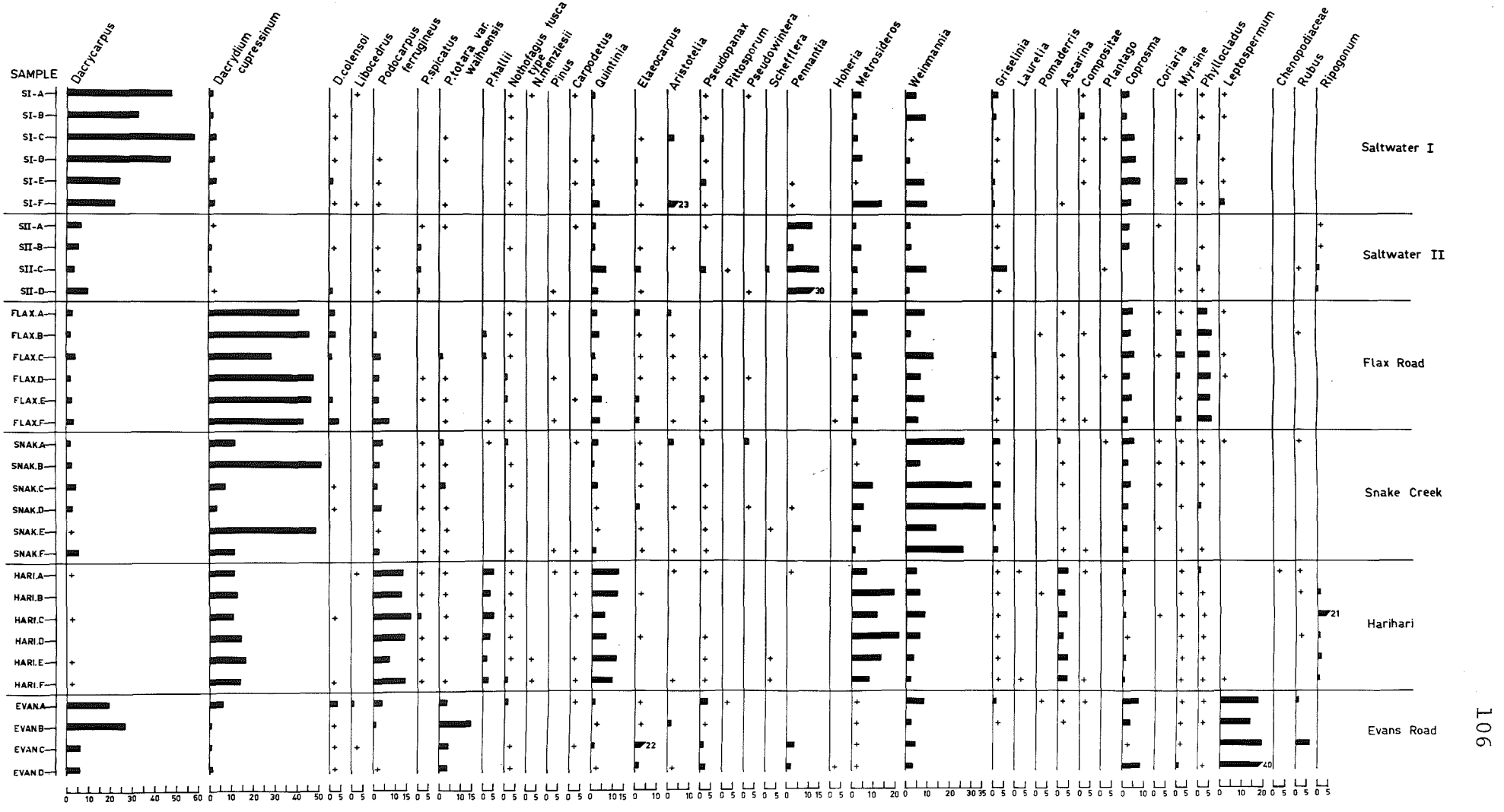
This site is in a stand of *Weinmannia racemosa* (55) with scattered podocarps of which *Dacrydium cupressinum* (12), *D. colensoi* (4) and *Dacrycarpus dacrydioides* (3.5) were the most important. The understorey is dominated by *Cyathea smithii* (6), *Dicksonia squarrosa* (5), *Pseudowintera colorata* (2.5), *Carpodetus serratus* (1.5), *Pennantia corymbosa* (1) and *Coprosma* spp. (0.5). A feature of the ground cover is the dense mat formed by *Nertera depressa*, *N. dichondraefolia*, *Metrosideros perforata* and numerous ferns. The forest at this site is degraded in places, by grazing and browsing animals and aggradation resulting from recent erosion of the hills above the site.

In contrast to the Flax Road sample the spectrum is influenced mainly by local source plants whose pollen exhibits low relative export. *Weinmannia* [23] and *Dacrydium cupressinum* [21] pollen are equally well represented in the

Figure 33. Pollen diagram for Harihari surface samples.

MODERN POLLEN RAIN, HARIHARI, WESTLAND

Pollen Sum: Total pollen and spores



SAMPLE
Gramineae
Astelia
Collospermum
Acaena
Umbelliferae
Taraxacum
Rumex
Ranunculus
Earina
Empodisma
Typha
Myriophyllum
Gunnera
Haloragis
Cyperaceae
Cyathea smithii
C.dealbata
Dicksonia squarrosa
D.lanata
Lycopodium
Phymatosorus
Pyrrosia
Gleichenia
Blechnum
Asplenium
Hymenophyllum
Monolete fern spores
Unidentified
SI-A
SI-B
SI-C
SI-D
SI-E
SI-F
SII-A
SII-B
SII-C
SII-D
FLAX.A
FLAX.B
FLAX.C
FLAX.D
FLAX.E
FLAX.F
SNAK.A
SNAK.B
SNAK.C
SNAK.D
SNAK.E
SNAK.F
HARI.A
HARI.B
HARI.C
HARI.D
HARI.E
HARI.F
EVAN.A
EVAN.B
EVAN.C
EVAN.D
17
Saltwater I
Saltwater II
Flax Road
Snake Creek
Harihari
Evans Road
+ = less than 1%

Snake Creek pollen spectrum despite the much greater basal area of *Weinmannia*. Much of the *D. cupressinum* pollen falls close to the source trees and this causes local over-representation. *Coprosma*, *Phymatosorus* and *Cyathea* are over-represented; *Dicksonia*, *Metrosideros* and *Pseudopanax* are proportionately represented and *Dacrycarpus*, *Dacrydium colensoi*, *Pseudowintera* and *Carpodetus serratus* are under-represented. Despite the dense herbaceous ground cover very little herb pollen was recorded.

5.4.5 Harihari (NZMS 1 S64 160022, Figures 28 and 31)

6 samples: HARI.A, HARI.B, HARI.C, HARI.D, HARI.E, HARI.F.

This site lies on a moderately steep slope behind the Harihari settlement. The canopy is dominated by *Podocarpus ferrugineus* (25), *Dacrydium cupressinum* (18), *Weinmannia racemosa* (41), *Quintinia acutifolia* (8) and *Elaeocarpus dentatus* (5). *P. ferrugineus* had a greater number of individuals but *D. cupressinum* trees were larger boled. The understorey is sparse with *Ascarina lucida* (1), *Hedycarea arborea* (1) and *Metrosideros umbellata* (1) as its major components. The ground cover has been browsed by goats and the recent extermination of them from the area has caused an upsurge in podocarp/hardwood regeneration accompanied by *Hymenophyllum* spp. and the slender lianes *Metrosideros diffusa* and *M. perforata*.

Pollen of *Podocarpus ferrugineus* [14], *Dacrydium cupressinum* [13] and *Metrosideros* [13] dominates the pollen spectrum. *Metrosideros* pollen is derived from three species so that its role in the pollen rain is difficult to assess. *Podocarpus hallii*, *Ascarina* and *Ripogonum* when near the sampling site are proportionately represented but *Weinmannia* and *Elaeocarpus*

are substantially under-represented. *Cyathea* spores are considered to have been derived by upward drift from gullies at lower altitudes where *C. smithii* was prominent.

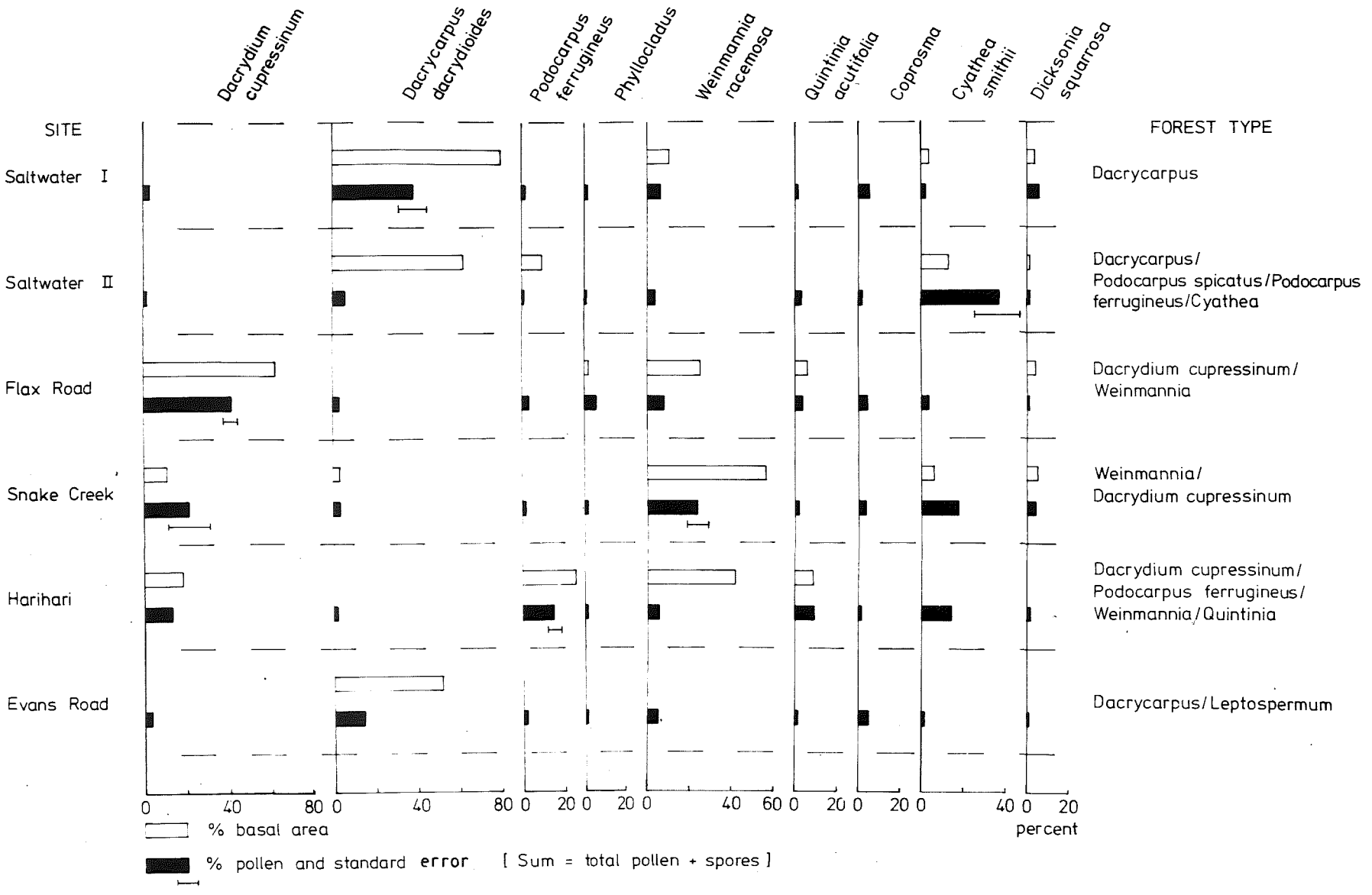
5.4.6 Evans Road (NZMS 1 S64 214102, Figures 28 and 32)

4 samples: EVAN.A, EVAN.B, EVAN.C, EVAN.D

Evans Road Bush is an association of shrubs and small trees. Covering about 21 ha and surrounded by pasture it is a last remnant of bush cover which once occupied large areas of the Wanganui River flood plain. *Dacrycarpus dacrydioides* (52) dominates the tree species accounting for 38 of the 100 trees and saplings measured in the vegetation survey. *Leptospermum scoparium* (30), *Pseudopanax* spp. (10) and *Pittosporum colensoi* (5) combine with *Dacrycarpus* to form an almost closed continuous canopy. *Podocarpus totara* var. *waihoensis* and *Dacrydium colensoi* are present around the fringes of the sampling area but are not included in the vegetation analysis. The understorey has been considerably disturbed by domestic animals and consists of ferns, *Libertia pulchella* and *Gleichenia*. An open pasture surrounds the Evans Road Bush.

Although *Dacrycarpus dacrydioides* is the dominant species in the area sampled the pollen spectrum is dominated by *Leptospermum* [23]. The presence of many immature individuals not yet contributing to the pollen rain may explain the under-representation of *Dacrycarpus*. Of the other taxa *Coprosma* is over-represented but exhibits wide sampling variability as does *Leptospermum* which is well represented. *Pseudopanax* and *Pittosporum* are under-represented. *Elaeocarpus*

Figure 34. Relationship between pollen rain and forest composition for main tree types, Harihari, South Westland.


Dacrydium cupressinum
Dacrycarpus dacrydioides
Podocarpus ferrugineus
Phyllocladus
Weinmannia racemosa
Quintinia acutifolia
Coprosma
Cyathea smithii
Dicksonia squarrosa
SITE
FOREST TYPE
Saltwater I
Dacrycarpus
Saltwater II
Dacrycarpus/ Podocarpus spicatus/Podocarpus ferrugineus/Cyathea
Flax Road
Dacrydium cupressinum/ Weinmannia
Snake Creek
Weinmannia/ Dacrydium cupressinum
Harihari
Dacrydium cupressinum/ Podocarpus ferrugineus/ Weinmannia/Quintinia
Evans Road
Dacrycarpus/Leptospermum
0 40 80
0 40 80
0 20
0 20
0 40 60
0 20
0 20
0 40
0 20
percent
% basal area
% pollen and standard error [Sum = total pollen + spores]

pollen [6] may have come from trees that have since disappeared from the bush as it is insect-pollinated and therefore not expected to have a good range of dispersal. A feature of the pollen spectrum is the pollen deposition from outside the immediate area with Gramineae [13] and, to a lesser degree, *Podocarpus totara* var. *waihoensis* [6.5] pollen the most frequently represented of the locally derived pollen types. *Weinmannia*, *Dacrydium cupressinum*, *Podocarpus ferrugineus*, *Cyathea* and *Quintinia* are consistently present and represent regional input.

5.5 DISCUSSION AND CONCLUSIONS

In order to estimate the relative pollen dissemination efficiencies (relative export) of the species present it is assumed that most of the pollen deposited has been derived from within a radius of *ca.* 1 km of the sampling site (i.e. no long distance transport). Taxa are discussed with reference to their pollen representation (i.e. over-, proportionately-, or under-represented), but it is emphasised that these categories may not necessarily hold in other spectra.

Dacrydium cupressinum is more or less proportionately represented in the pollen spectra but there are exceptions. Representation of *D. cupressinum* pollen at Harihari and Snake Creek compared to basal area figures differs with respect to the trunk space component. Local over-representation at these two sites is attributable to the density of trees and an almost closed canopy restricting air circulation. These differences are reflected in large standard errors for the mean pollen percentage of *D. cupressinum*. The relatively low

frequencies of *D. cupressinum* pollen at three sites (Saltwater I and II, Evans Road), especially in a region where it is the dominant species, appear, at first sight to contradict earlier work. Moar (1970) reported the transport of *D. cupressinum* pollen from Westland to Canterbury, and Mildenhall (1976) has noted *D. cupressinum* pollen on Chatham Island derived from mainland New Zealand, 725 km to the west. Therefore, although *D. cupressinum* has widely dispersed pollen local representation is strongly affected by vegetation structure and the characteristics of pollen production and dispersal of other taxa in the vegetation. The percentages of *Dacrycarpus dacrydioides* pollen recorded at all sampling sites are all lower than the per cent basal area. This under-representation, also reported by Harris and Fisher (1947), may result from low pollen production. At Saltwater II and Harihari *Podocarpus ferrugineus* is under-represented probably resulting from masking by over-represented locally abundant species. The low frequencies recorded at the other sites illustrate the regional presence of the species but indicate little of its importance in the vegetation of the region. According to Moar (1970) *Phyllocladus* is over-represented when present at the sampling site. This view is substantiated by the data from Flax Road. Relatively low pollen frequencies at the remaining sites reflect the scattered and limited distribution of *Phyllocladus* in the study area.

Weinmannia racemosa flowers profusely and is insect-pollinated (Wardle 1966). Moar (1970) considers this pollen to be under-represented, an observation supported by results obtained in this study. The disparity between basal area

and pollen percentages for *Weinmannia* point out the comparative pollen dissemination capabilities of insect and wind-pollinated plants. *Quintinia acutifolia*, the second most important hardwood in the regional vegetation, is proportionately represented in the pollen spectra. Moar (1970) noted *Quintinia* pollen in surface samples on the Fox Range, Westland, apparently derived from lower altitudes. It appears at least from field observations that *Quintinia* flowers most years, however its entomophilous flower suggests low pollen production (Faegri and van der Pijl 1971). These results would argue that *Quintinia* may rely on both insects and wind for pollen dissemination. *Coprosma* was over-represented at all sampling sites. This is not surprising as *Coprosma* is anemophilous but at least part of the over-representation can be due to the tendency of basal area measures to under-represent small stemmed trees or shrubs (Whitehead and Tan 1969). *Coprosma* pollen cannot be identified to species level and it is therefore difficult to assess the role of individual species in the pollen rain.

Cyathea smithii is consistently over-represented. At Saltwater II there is extreme variation between samples suggesting heavy spore production and relatively poor dispersal. Dodson (1976) noted a similar phenomenon with *C. dealbata*. This supports the conclusion reached by Raynor, Ogden and Hayes (1976) that fern spores are lost from the atmosphere faster due to their larger size and greater gravitational settling velocity. *Dicksonia squarrosa* has low basal area at most sites and is proportionately represented without displaying widespread dispersal capabilities.

Pollen percentages of *Pennantia corymbosa* and *Ascarina*

lucida slightly exceed the per cent basal area recorded and the pollen percentages of *Leptospermum* and *Griselinia* are equal to or slightly less than their per cent basal area, but *Pennantia* and *Leptospermum* exhibit wide sampling variability (Table 7) and therefore low relative export. Within the limits of the accuracy of this study, all these genera have similar pollen representation. The pollen percentages of *Dacrydium colensoi* at Snake Creek and *Podocarpus spicatus* at Saltwater II scarcely reflect their importance at these localities. *Pseudopanax, Elaeocarpus, Pittosporum, Myrsine, Carpodetus serratus* and *Pseudowintera* are under-represented but this may be expected as they are all entomophilous. Contrary to this work, Dodson (1976) found *Myrsine* to be over-represented in low woodland formations of low pollen production on the Chatham Islands. This vegetation must resemble the *Myrsine - Coprosma* shrubland of initial post-glacial times in Canterbury and Westland (Moar 1971), because on the basis of the present results it is difficult to envisage *Myrsine* attaining high pollen frequencies in anything but shrub vegetation in which it is dominant. *Metrosideros* was recorded consistently with most of the pollen contributed by the lianes *M. perforata* and *M. diffusa*. Wardle (1971) reports that some pollen from *M. umbellata* becomes airborne but most falls close to the source trees; the pollen frequency (1%) at Harihari where this species was present is probably a direct result of this. Very low frequencies (1%) of *Nothofagus fusca* type pollen are recorded at all sampling sites. *Nothofagus* forest is absent from the area so pollen has probably been derived from forest east of the Main Divide (Moar 1973)

At most sites *Nertera* provided a patchy but dense ground cover, however pollen of this genus is absent from all surface spectra. *Nertera* pollen sometimes loses its gemmae and could then be confused with *Coprosma* pollen. Pollen of the wind-pollinated families Cyperaceae and Gramineae is consistently recorded and originates from the non-forested pasture regions of the river flats between the Wanganui and Poerua Rivers. Spores of most ferns are detected in low frequencies b[illegible] local over-representation of *Hymenophyllum* and *Phymatosorus* was noted.

There are serious drawbacks in the use of R-values (Table 7). Extreme variation in the values obtained from some species (e.g. *Coprosma*, *Griselinia*, *Pennantia*) may result from limitations of a vegetation survey which does not adequately account for shrub species. Accurate vegetational data must be available for a very large area to prevent irregularities in R-values (Livingstone 1968) and also their use ignores the differential effect of varying distances on pollen dispersal (Oldfield 197[illegible]). The R-values do serve to illustrate local over-representation and therefore local presence of some species (e.g. *[illegible]gdium cup[illegible]essinum* at Snake Creek, *Pennantia corymbosa* at Sa[illegible]water II, *Ascarina lucid[illegible]* at Harihari, *Phyllocladus alpinus* at [illegible] Road and *Coprosma* at Saltwater I), nevertheless, it is concluded that only limited use can be made of R-v[illegible]lues in Westland. The wide variety of vegetation types in this regio[illegible] prohibit any widespread application of R-v[illegible]es as a means of correcting pollen rain percentages.

Wind-pollinated taxa ar[illegible] proportio[illegible]ately represented or over-represented when compa[illegible] with ins[illegible]ect-pollinated

taxa. There are exceptions, the most notable of which are *Podocarpus ferrugineus*, *P. spicatus*, *Dacrydium colensoi* and *Dacrycarpus dacrydioides*. Low pollen frequencies of these species do not imply their rarity in the vegetation, and high frequencies suggest their presence at the site of deposition. The insect-pollinated plants *Weinmannia*, *Metrosideros* and *Elaeocarpus* are under-represented outside the vegetation in which they occur. Similarly, low frequencies of these genera cannot be taken to indicate their absence from the sampled area. Surprisingly, dispersal of *Dacrydium cupressinum*, *Leptospermum*, *Phyllocladus*, *Coprosma* and *Cyathea smithii* away from the forest in which they occur is restricted. Despite large areas of pasture and swampland in the surrounding area (Figure 28) only modest amounts of Gramineae and Cyperaceae pollen are recorded which suggests that there is only limited pollen transport into and through forested areas. Because the samples were taken in small openings or under the canopy the local vegetation probably inhibits run-out of pollen from the regional vegetation.

CHAPTER 6

MODERN POLLEN RAIN FROM VARIOUS SOUTH ISLAND LOCALITIES

6.1 INTRODUCTION

In November 1975 Mr M.S. McGlone collected five surface samples from Ajax Hill in South-east Otago. A pollen analysis of these samples suggested that *Phyllocladus*, *Libocedrus* and *Dacrydium biforme* gave anomalous pollen distribution patterns. To interpret the results, from these ecologically important species, with greater precision further sampling was carried out. This was done in the environs of the Moa Stream, a tributary of the Wilberforce River in Canterbury and the Kelly Range near Otira in Westland. At these two sites the three gymnosperms were abundant and it was possible to compare their pollen representation when they were growing together and also when in association with other forest trees, notably *Nothofagus*. Surface samples were also obtained from the Old Man Range, Central Otago, Meins Knob in the upper reaches of the Rakaia River, and Stewart Island.

The general localities of the sampling stations are shown on Figure 3 while the locations of each sample are shown on locality maps drawn for each station. The pollen frequencies of all taxa noted in the samples are recorded in Figure 36, and these have been calculated on a base sum of total pollen and spores excluding over-represented local types where necessary. These have been noted on Figure 36.

6.2 AJAX HILL STUDY AREA

6.2.1 Introduction

Ajax Hill (NZMS 1 S178 152019) is part of an undulating plateau which rises to 720 m and forms the highest part of the generally forested Catlins region in South-east Otago. Johnson, Mark and Bayliss (1977) have described the vegetation at Ajax Hill in some detail. The area comprises a mosaic of bog, flush and scrub-woodland communities about 1 km^2 in extent (Figure 35). Surface samples from the different communities on and surrounding the bog and the vegetation at these sites will be described in 6.2.4.

6.2.2 Vegetation Surrounding Ajax Hill

The regional vegetation consists of forest dominated by *Weinmannia racemosa*. *Weinmannia* is associated with podocarps at lower altitudes and co-dominates with *Metrosideros umbellata* at higher altitudes. *Nothofagus menziesii* forest occupies the upper Maclennan Valley east of Ajax Hill and parts of the adjacent Catlins Valley with several isolated stands in the Tahakopa Valley to the south-west. The forest in the floor of the Tahakopa Valley is mostly *W. racemosa* with *Dacrycarpus dacrydioides*, *Podocarpus spicatus* and *Dacrydium cupressinum*. Underneath this canopy is *Cyathea smithii*, *Neomyrtus pedunculata*, *Coprosma foetidissima* and *C. colensoi*. At a higher altitude *W. racemosa* remains dominant with occasional *Griselina littoralis*, *Pseudopanax crassifolius* and *Carpodetus serratus* sharing the canopy. *Coprosma* spp. form a dense understorey. At *ca.* 500 m altitude *Leptospermum scoparium* woodland replaces the *W. racemosa*. Above this zone is scrub with *L. scoparium*, *Dracophyllum longifolium*, stunted specimens of *Libocedrus bidwillii*, tussocks

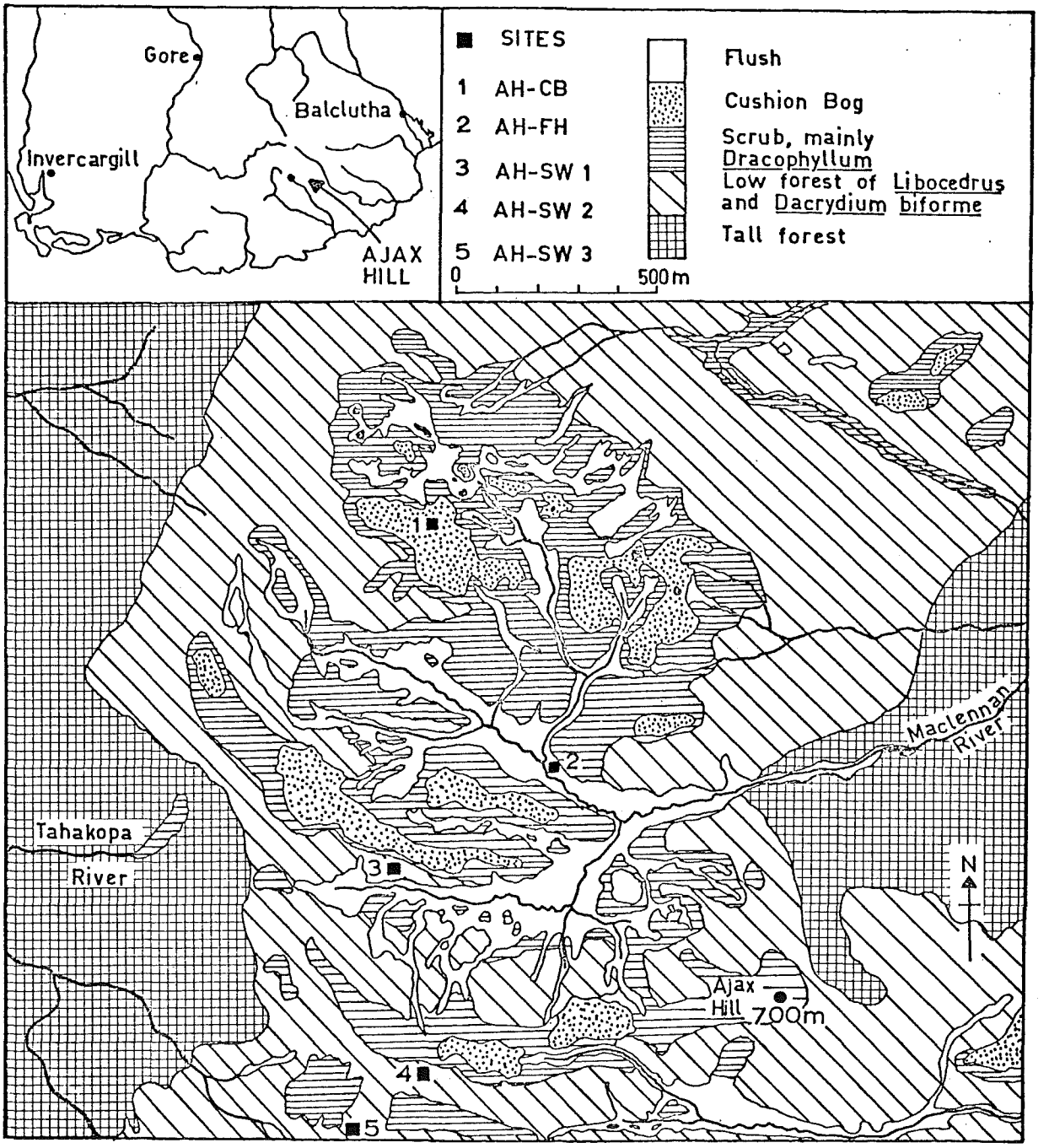


Figure 35. Vegetation and location of sites at Ajax Hill. Inset: South-east Otago and Southland; study area arrowed. Redrawn, with permission from Johnson, Mark and Bayliss (1977).

of *Gahnia procera* and large tufts of *Phormium cookianum*. At the crest of the hill near 600 m *Dacrydium biforme* becomes co-dominant with *Dracophyllum* and *Libocedrus bidwillii* forming a dense woodland vegetation characteristic of the tablelands surrounding Ajax Hill.

6.2.3 Vegetation at each Sampling Site

a. AH-CB: The site sampled lay in cushion bog. Johnson *et al.* (1977) provide mean percentage cover for species on and around the site. Important among these and listed in descending order of importance are *Leptospermum scoparium*, *Dracophyllum longifolium*, *Cyathodes empetrifolia*, *Coprosma pumila*, *Pentachondra pumila*, *Donatia novae-zelandiae*, *Celmisia gracilenta*, *Chionochloa rubra*, *Dacrydium biforme*, *Empodisma minus*, *Lycopodium ramulosum* and *Oreobolus strictus*. Some with low cover values but very abundant include: *Dacrydium laxifolium*, *Gentiana lineata* and *Pernettya macrostigma*.

b. AH-FH: This site is in open flush vegetation (Johnson *et al.* 1977). Locally *Dracophyllum longifolium*, *Chionochloa rubra*, *Pernettya macrostigma*, *Coprosma pumila*, *Hebe odora*, *Pentachondra pumila* and *Sphagnum* were abundant. *Dacrydium biforme* and *Phyllocladus alpinus* scrubland is near the sampling site to the north.

c. AH-SW 1: This sample was collected in a 5 x 2 m clearing in a scrub-woodland community. *Dracophyllum longifolium* (31.9% cover, Johnson *et al.* 1977), *Dacrydium biforme* (14.6%), *Coprosma foetidissima* (13%), *Phyllocladus alpinus* (9.8%) and emergent *Libocedrus bidwillii* (5.5%) are the major components. *Coprosma astonii*, *Cyathodes empetrifolia* which covers small clearings, *Hymenophyllum multifidum* and *Luzuriaga parviflora*

are common in the understorey.

d. AH-SW 2: Thick *Phyllocladus alpinus - Dacrydium biforme* scrub surrounded this surface sample. The understorey is dominated by *Dracophyllum longifolium*, *Gahnia procera* and *Coprosma* spp.

e. AH-SW 3: The sample lay in an area of dense *Myrsine divaricata* scrub with *Coprosma* spp., *Dracophyllum longifolium* and the other major scrub species present at SW1 and SW2.

6.2.4 The Pollen Rain

In the surface samples analysed from Ajax Hill only Gramineae and *Coprosma*, of the locally derived pollen types, are consistently recorded. At each site Gramineae contributes up to 20% of the total pollen and *Coprosma ca.* 5%. At AH-CB site *Lycopodium ramulosum* is over-represented with 10% of the total pollen. A consequence of poor local representation is that a great proportion of the pollen is derived from anemophilous trees growing in montane or lowland forests. Their pollen is probably transported upwards prior to dispersal and included in this category are *Dacrydium cupressinum*, *Podocarpus spicatus*, *Pinus* spp., *Nothofagus fusca* type, *N. menziesii* and spores of *Cyathea smithii*.

The scrub-woodland elements reveal inconsistent and discontinuous pollen representivities. This is probably due to their low relative export and the low pollen production of the species they are associated with. On the other hand the Ajax Hill spectra give no indication, at least in terms of pollen percentage, that the montane forest in the Maclennan and Tahakopa Valleys is dominated by *Weinmannia racemosa* and (at higher altitudes) by *Metrosideros*

Figure 36. Pollen diagram for South Island surface samples. The pollen sum was total pollen and spores except for the following exclusions:

Compositae	at	MOAST-1
Muehlenbeckia	at	MOAST-3, NTHST
cf. *Discaria*	at	WILBFN
Cyperaceae	at	MKB-T

MODERN POLLEN RAIN

Pollen Sum: Total pollen and spores

SAMPLE

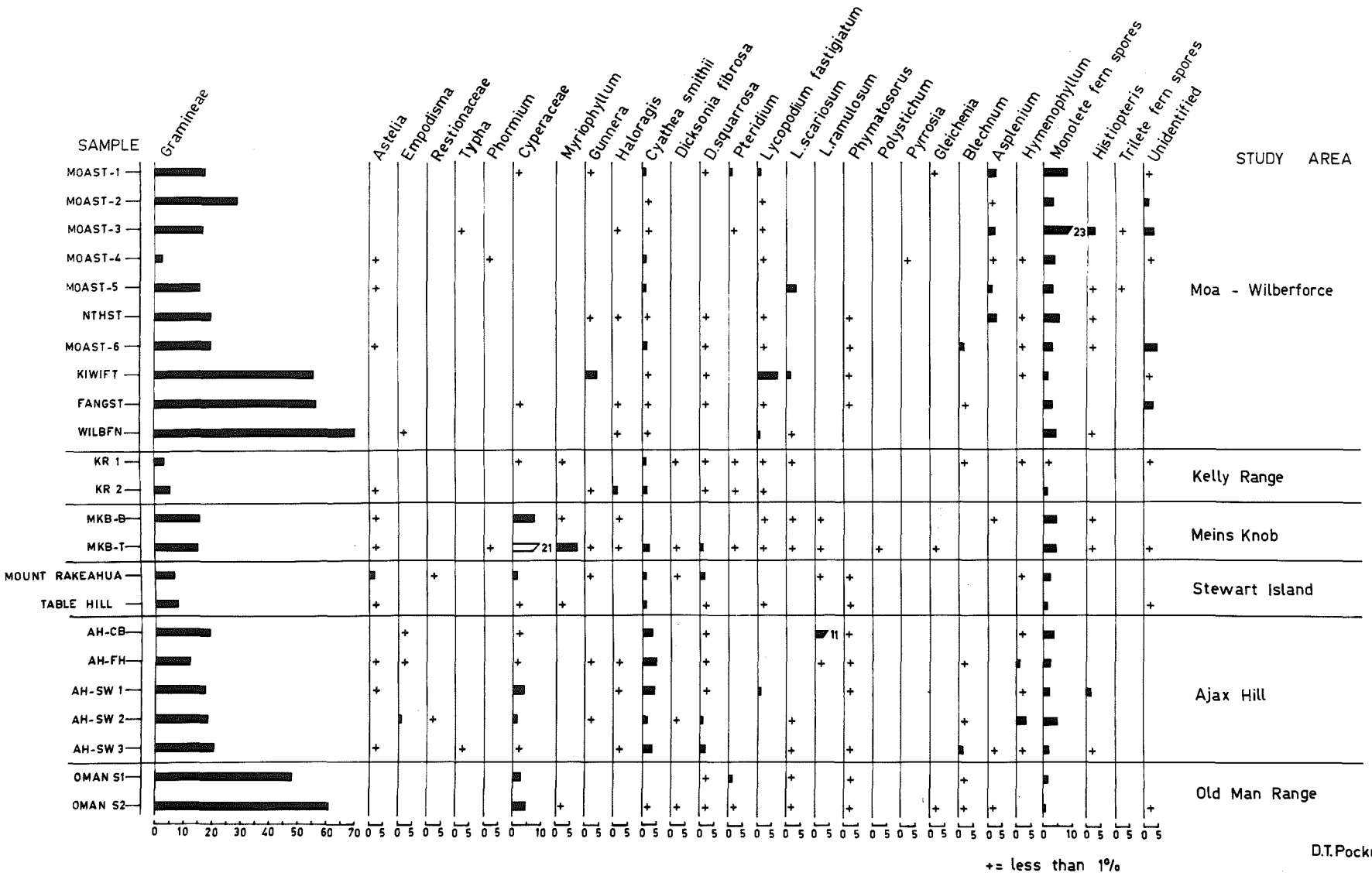
Dacrycarpus
Dacrydium cupressinum
D.colensoi
Libocedrus
Podocarpus ferrugineus
P.spicatus
P.hallii
Nothofagus fusca type
N.menziesii
Pinus
Myrtaceae
Carpodetus
Quintinia
Elaeocarpus
Aristotelia
Pseudopanax
Pseudowintera
Pennantia
Metrosideros
Weinmannia
Griselinia
Ascarina
Compositae
Plantago
Coprosma
Coriaria
Myrsine
Scrophulariaceae
Pentachondra
Phyllocladus
Dacrydium intermedium
D.bidwillii/biforme
Leptospermum
Salix
Cyathodes
Chenopodiaceae
Muehlenbeckia
Epilobium
Drapetes
cf. Discaria
Umbelliferae
Cruciferae
Taraxacum
Rumex
Ranunculus

STUDY AREA

Sample	Study area
MOAST-1	Moa - Wilberforce
MOAST-2	
MOAST-3	
MOAST-4	
MOAST-5	
NTHST	
MOAST-6	
KIWIFT	
FANGST	
WILBFN	
KR 1	Kelly Range
KR 2	
MKB-B	Meins Knob
MKB-T	
MOUNT RAKEAHUA	Stewart Island
TABLE HILL	
AH-CB	Ajax Hill
AH-FH	
AH-SW 1	
AH-SW 2	
AH-SW3	
OMAN S1	Old Man Range
OMAN S2	

28
55
61
22
63

0 5 0 10 20 30 0 5 0 10 20 0 10 0 10 0 10 0 10 20 30 40 45 0 10 0 10 0 5 0 5 0 5 0 5 0 5 0 10 15 0 5 0 5 0 5 0 5 0 5 0 10 15 0 5 0 5 0 5 0 10 0 5 0 5 0 5 0 5 0 10 20 30 40 45 0 5 0 10 0 5 0 5 0 5 0 5 0 10 0 5 0 5 0 10 0 5 0 5 0 5 0 5 0 10



D.T.Pocknall 1978

umbellata.

Nothofagus fusca type and *N. menziesii* are recorded in more or less equal pollen frequencies (*ca.* 7%). Pollen of *N. fusca* type has had to travel much greater distances (probably from the Longwood Range about 120 km to the west) than that of *N. menziesii* which is abundant in the upper Maclennan Valley. This indicates the difference in the relative dissemination capabilities of the two *Nothofagus* pollen types previously reported by McKellar (1973).

The cushion bog and flush vegetation consist mainly of low growing, mostly entomophilous, and hence low pollen producing shrubs or herbs, and their pollen is rarely encountered above trace frequencies. Nevertheless when observed they often signify the presence and possible importance of species whose ecological and climatic tolerances testify to the environment from which the sample originated. Included among these in this area are *Cyathodes*, *Pentachondra*, Umbelliferae, Cruciferae, *Drapetes*, *Rumex* and *Epilobium*. Due to the low pollen output of the local types *Dacrydium biforme* is shown to be well represented in sample AH-FH when it is generally poorly represented in other samples. At this site also, *Podocarpus spicatus* contributes 11% of the total pollen and *Dacrydium cupressinum* 15%, further emphasising the low pollen production of the flush vegetation. *Libocedrus* is poorly represented (*ca.* 1%) in AH-FH and therefore exhibits low relative export.

Dracophyllum longifolium which is widespread on Ajax Hill is barely recorded except at AH-SW3, and to a lesser degree AH-SW1, where its true importance in the vegetation is more correctly shown. However, this is probably understandable

as *Dracophyllum* is entomophilous. Although *Phyllocladus* is locally abundant the pollen of this wind pollinated shrub is recorded infrequently (<5%) therefore giving little impression of its local importance. Other under-represented pollen types are *Leptospermum scoparium*, *Myrsine* and somewhat surprisingly the restiad *Empodisma minus* which is very abundant on the cushion bog.

Notable occurrences in the pollen rain, and doubtless derived by uplift from plants at lower altitudes are *Carpodetus*, *Pseudowintera*, *Elaeocarpus*, *Pennantia* and *Griselinia*.

6.3 MOA STREAM-WILBERFORCE RIVER STUDY AREA

6.3.1 Introduction

The Wilberforce River meets the Rakaia River south-west of Lake Coleridge. The vegetation of the region has not been extensively surveyed except for the broad description provided by Wardle (1970) and the floral list for the upper and lower Wilberforce catchments provided by Burrows (1977). In the lower reaches of the Wilberforce River the forests are mainly restricted to the catchments of the tributary streams. Elsewhere the vegetation is tussock and low scrub with *Phyllocladus alpinus* and *Discaria toumatou* prominent. *Nothofagus solandri* var. *cliffortioides* is the main tree species but up to *ca.* 920 m altitude there are scattered areas of *Podocarpus hallii*, *Libocedrus bidwillii* and *Dacrydium biforme*; especially in the catchment of Unknown Stream. *N. menziesii* is absent and there is very little *N. fusca*. Due to repeated burning it is difficult to define an upper limit for *N. solandri* var. *cliffortioides* but in the

lower Wilberforce Valley it does form an apparently natural timberline around 1300 m. Above this altitude there is low subalpine scrub of *Phyllocladus alpinus* and *Podocarpus nivalis*.

Broad vegetational units are mapped on Figure 37 which also shows the location of the surface samples. The map has been redrawn from NZMS 1 S65 (Wilberforce) and the sites selected from aerial photographs (run 3727/3 and 4) taken in 1964. Figure 38 shows the confluence of the Moa Stream and Wilberforce River.

6.3.2 Vegetation and Pollen Rain at each Sampling Site

a. MOAST-1 (*ca.* 730 m): A surface sample of *Raoulia - Rhacomitrium* was collected in an open site on old river terrace (NZMS 1 S65 784057) on the flank of the Moa Stream. The predominant vegetation is forest of *Nothofagus solandri* var. *cliffortioides* with *Libocedrus bidwillii* and *Podocarpus hallii* on both sides of the Moa Stream. Further up the stream opposite the Pukeko Stream *Phyllocladus alpinus* merges with the *N. solandri* var. *cliffortioides* (Figure 39) which becomes lower in stature and less densely distributed. Locally there are patches of grassland, mainly *Poa laevis*.

The pollen spectrum provides a good assessment of the regional vegetation. *N. fusca* type (which includes *N. solandri* var. *cliffortioides*) and Gramineae pollen are the most abundant if the over-represented Compositae is excluded from the base sum. The composite pollen were small with minute spines and were probably those of *Raoulia* which formed part of the surface sample. The surrounding vegetation is well recorded, a phenomenon not previously observed in an area where

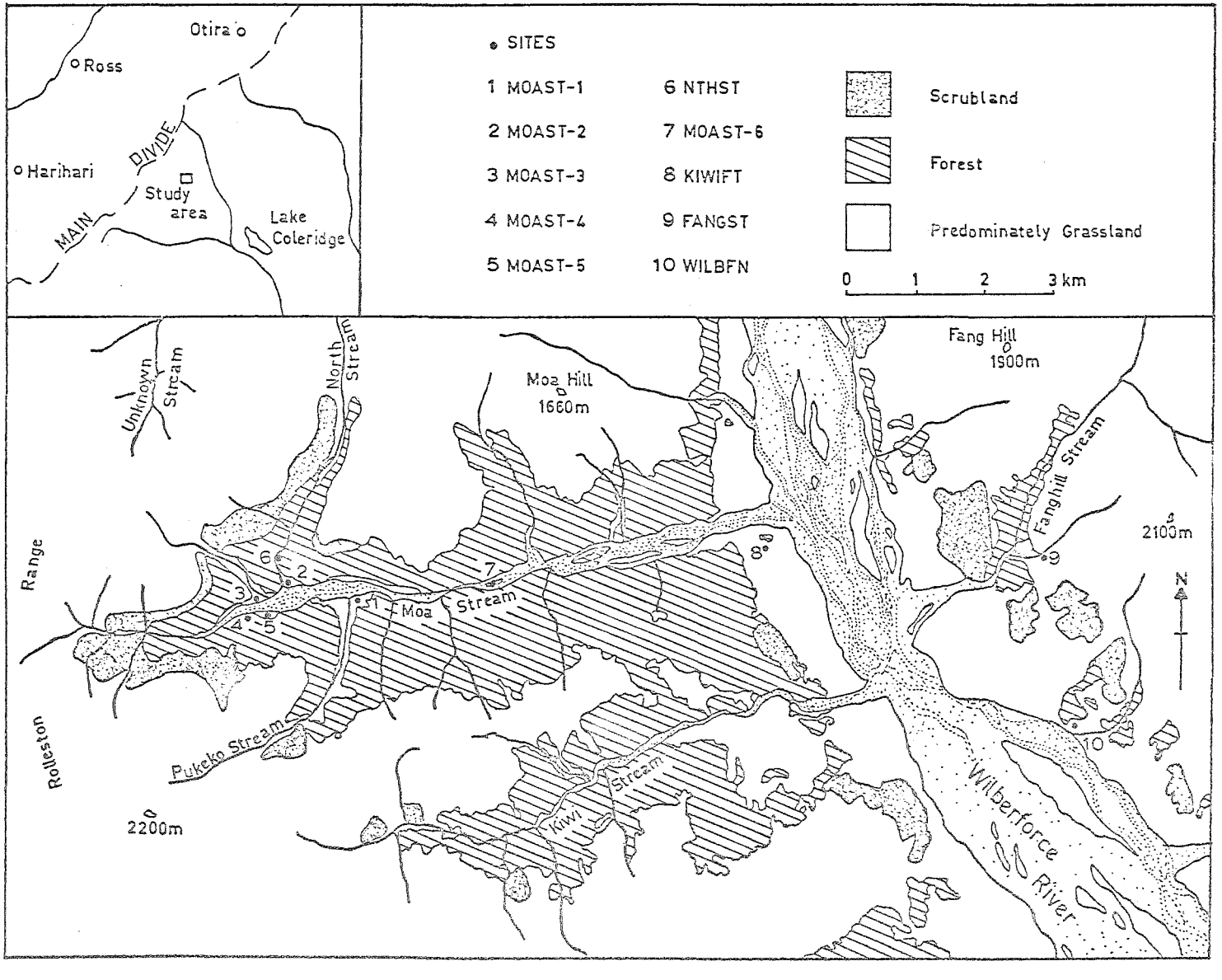


Figure 37. Location of sites in the Moa Stream - Wilberforce River region, Canterbury. Inset: Canterbury and Westland; study area marked.

Figure 38. The confluence of the Wilberforce River and Moa Stream from the northern bank of the Wilberforce. Kiwi Flat (arrowed) is in the middle distance and the Rolleston Range in the background.

Figure 39. The transition from *Nothofagus solandri* var. *cliffortioides* forest to *Phyllocladus alpinus* shrubland in the catchment of Pukeko Stream, a tributary of Moa Stream.

Nothofagus fusca type species are dominant. *Phyllocladus* contributes 12% of the total and *Dacrydium biforme* shows good export of pollen from the Unknown Stream catchment to be recorded in a >5% frequency. *Coprosma*, *Asplenium* and monolete fern spores represent the understorey component of the adjacent forest.

There is apparently a low frequency of pollen imports but these include *Dacrydium cupressinum* (4.5%) which is rare in Canterbury vegetation (Franklin 1968); *Podocarpus ferrugineus* (1.5%); *P. spicatus* (1%); *Dacrycarpus* (1%) and *Cyathea smithii* (<1%). These have obviously passed over the Main Divide from Westland forests although *P. spicatus* may be derived from Mt Algidus 2 km downstream of the Moa Stream. *Pinus* (3%) has also probably originated in this region.

b. MOAST-2 (*ca.*750 m): This site lay in an open grassland area of 20 x 15 m near the N.Z. Forest Service Cedar Hut (NZMS 1 S65 776058). The clearing is surrounded by *Phyllocladus alpinus*, *Libocedrus bidwillii*, *Olearia ilicifolia*, *Dracophyllum traversii*, *Coprosma parviflora*, *Muehlenbeckia australis* and *Podocarpus nivalis*. All species were more or less of equal abundance at the site but the dominant forest vegetation which was only 30 m distant contained *Nothofagus solandri* var. *cliffortioides* and *Phyllocladus alpinus*.

Locally derived pollen dominates the spectrum with *Phyllocladus* (36%), Gramineae (29%) and *Muehlenbeckia* (9%) the most notable. *Libocedrus* and *N. fusca* type are considerably under-represented. Violent fluctuations in the representation of *Nothofagus fusca* pollen which is presumably *N. solandri* var. *cliffortioides* suggests that it is not as well recorded as are other *N. fusca* type species. Poole (1948) reports that

Nothofagus flowers less frequently at higher altitudes and thus it may not be recorded from a sample scanning only 4-5 years of pollen rain. The same situation could well exist for *Libocedrus* but this pollen is frequently under-represented (Moar 1971) and under certain conditions is not well preserved. *Dacrydium biforme* is barely recorded which suggests extreme variability in the pollen representation of this species. The proportion of pollen transported from the west is minimal but this is no doubt due to the higher producing local types, *Phyllocladus alpinus* and Gramineae, concealing their presence.

Olearia ilicifolia, *Dracophyllum traversii* and *Podocarpus nivalis* are significantly under-represented. The paucity of *P. nivalis* pollen is interesting; it is a consistently high pollen producer, but either its pollen is poorly preserved or the low prostrate stature of the plant restricts its dissemination capabilities.

c. MOAST-3 (*ca.* 780 m): This sample was collected in the centre of an old fan (NZMS 1 S65 771057) which has been revegetated with *Olearia ilicifolia*, *Muehlenbeckia australis*, *Coprosma parviflora*, *C. rugosa*, *Polystichum vestitum* and tussock grasses (Figure 40). *Phyllocladus alpinus* is frequent at the site but the nearest forest vegetation is 200 m to the north where there is *Libocedrus bidwillii*, *P. alpinus*, and *Podocarpus hallii*. *Nothofagus solandri* var. *cliffortioides* is nearly 400 m from the collection site.

Pollen of *Muehlenbeckia* dominated the spectrum and has been excluded from the sum. Monolete fern spores (presumably *Polystichum vestitum*, 23%), Gramineae (17%), *Phyllocladus* and and *Coprosma* (8%) are the main contributors to a spectrum

Figure 40. Scrub dominated by *Olearia ilicifolia* at the site of MOAST-3. *Libocedrus bidwillii* dominates the forest in the right of the picture.

Figure 41. Low forest of *Phyllocladus alpinus*, *Libocedrus bidwillii*, *Podocarpus hallii* with numerous hardwoods at the site of MOAST-4.

which mirrors the local vegetation with the exception of the under-represented *Olearia ilicifolia*. The sample contained a low value (8%) of regional forest pollen but this percentage would be easier to assess and better represented if all the local sources were removed from the pollen sum. Locally growing herbaceous plants contributed little to the total, only *Rumex* (3%) and Umbelliferae (2.5%) being recorded.

d. MOAST-4 (*ca.* 790 m): The sample came from within low forest on the eastern flank of Moa Stream (NZMS 1 S65 770054) (Figure 41). The dominant species are *Phyllocladus alpinus* and *Libocedrus bidwillii* with *Pseudopanax lineare*, *Dracophyllum traversii*, *Archeria traversii*, *Griselinia littoralis* and *Podocarpus hallii* also prominent. The principal components in the low understorey are *Coprosma parviflora*, *Myrsine divaricata* and *Gleichenia circinata*.

The pollen spectrum reflects the dominance of *Phyllocladus alpinus* (52%), *Pseudopanax* (16%) and *Libocedrus* (9.5%) in the local vegetation. *Griselinia*, *Coprosma* and *Myrsine* are also well recorded. The epacrids, *Dracophyllum* and *Archeria* are both under-represented but they are insect-pollinated. There is a very low export of pollen into the sampled vegetation with *Nothofagus fusca* type providing 2% and Gramineae 3% of total pollen.

e. MOAST-5 (*ca.* 750 m): An open area (NZMS 1 S65 772054), consisting mainly of *Poa caespitosa* was sampled. Locally, herbaceous plants including *Raoulia* and the fern *Lycopodium scariosum* are important. The nearest tree-shrub species are to the south but only 20 m away. These included *Phyllocladus alpinus*, *Libocedrus bidwillii*, *Podocarpus hallii* and *P. nivalis*.

The open nature of the site would allow good representation of the regional and extra local pollen sources, although local Gramineae (16%), Compositae (14%) and *Lycopodium* (3%) are important. The predominance of *Phyllocladus* in the immediate regional vegetation and *Nothofagus solandri* var. *cliffortioides* is shown by pollen frequencies of 22% and 10% respectively. *Libocedrus* and *Podocarpus hallii* show limited dispersal distance under these conditions. The regional component of the pollen rain is shown in imports of *Dacrydium cupressinum* (2%), *Podocarpus ferrugineus* (1%), *Pinus* (1%) and *Cyathea smithii* (1%). The low values of *Epilobium* pollen testify to its presence at the site of deposition.

f. NTHST (*ca.* 820 m): The vegetation at this site (NZMS 1 S65 772062), on the margins of North Stream, consists of a mosaic of *Coprosma - Dracophyllum* shrubland. Scattered among this are *Muehlenbeckia australis*, *Griselinia littoralis*, *Olearia ilicifolia*, *Cyathodes colensoi* and *Coriaria plumosa*. Surrounding the site on the steep slopes above North Stream are extensive tracts of *Phyllocladus alpinus* and *Libocedrus bidwillii* forest.

Muehlenbeckia was much over-represented and was therefore excluded from the pollen sum, nevertheless this pollen is shown to be derived from a local source with low relative export. Gramineae (20%), *Phyllocladus* (16%) and *Coprosma* (16%) provide the bulk of the pollen. *Libocedrus* (6.5%) is reasonably well represented as is *Nothofagus fusca* type pollen (7.5%). *Dracophyllum* is severely under-represented while *Griselinia* and Compositae are rarely seen. In contrast to *Raoulia* in sample MOAST-1, *Olearia ilicifolia* here appears to produce little pollen. About 5% of the total is imported,

the most notable being *ca.* 1% *Dacrycarpus* pollen.

g. MOAST 6 (*ca.* 700 m): This sample was collected on an old river bed (NZMS 1 S65 807059) on which there is tussock grassland of *Poa caespitosa* and *P. colensoi*; herbaceous vegetation with *Raoulia tenuicaulis*, *Linum monogynum* and *Ranunculus lappaceus* prominent and shrubs including *Parahebe decora*, *Cyathodes colensoi* and *Coprosma rugosa*. Almost completely surrounding the sampling site is forest dominated by *Nothofagus solandri* var. *cliffortioides*.

The pollen spectum shows elements of both the local and regional pollen rain. *Nothofagus fusca* type (45%) dominates and thus represents the major regional vegetation while pollen frequencies of 20% for Gramineae and 8% for Compositae provide a local component. This site is only 3.5 km north of samples b. - f. and yet *Phyllocladus* and *Libocedrus* are recorded in barely trace frequencies. This not only supports the already intimated low relative export of *Libocedrus* but also suggests that *Phyllocladus* pollen is not dispersed very far. In this case though, the small size of the source plants and the abundance of *Nothofagus* pollen are obvious factors in its poor representation.

h. KIWIFT (*ca.* 625 m): At this site, situated on Kiwi Flat (Figure 38) alongside the Wilberforce River (NZMS 1 S65 850065) there is an almost complete plant cover. It is dominated by *Poa caespitosa* and interspersed with this species are *Anisotome aromatica*, *Mentha cunninghamii*, *Gunnera albocarpa*, *Ranunculus lappaceus*, *Viola cunninghamii*, *Cyathodes colensoi* and *Lycopodium scariosum*. To the west, 50 m away, is a dense stand of *Discaria toumatou* and due south, *ca.* 200 m distant, is

the front of an extensive forest of *Nothofagus solandri* var. *cliffortioides* (which was in flower, i.e. summer of 1977/78).

Gramineae pollen (55%) is dominant. The herbaceous pollen contribution is small in total and consists of 4% *Gunnera*, 3% Compositae, 2% Cruciferae, 2% Umbelliferae and 8% *Lycopodium* spores. *N. fusca* type (9%) is surprisingly infrequent considering its nearness and flowering state and the time of sampling. *Discaria* pollen is recorded in low levels suggesting poor production and dispersal; *Discaria* belongs to the Rhamnaceae so it is probably insect-pollinated. The low frequency of *Phyllocladus* (3%) suggests its scattered regional distribution. In this instance it is probably derived from an upstream source having arrived at the site of deposition through the prevailing westerly winds.

i. FANGST (*ca.* 950 m): *Podocarpus hallii* and tussock grasses are the major components of the vegetation surrounding this site (NZMS 1 S65 894064) which lay in the upper reaches of a small tributary of Fanghill Stream on the north side of the Wilberforce River. Plant cover is irregular due to erosion and consists mainly of *Hoheria glabrata*, *Phyllocladus alpinus*, *Griselinia littoralis*, *Coprosma parviflora*, *Dracophyllum uniflorum*, *Hebe odora*, *Phormium cookianum* and *Blechnum vestitum*.

This sample was collected primarily to test the representation of *Podocarpus hallii*. It seems that locally *P. hallii* is more-or-less proportionately represented, however its relative export is poor and it is often scarcely recorded >50 m from the parent trees. In this particular instance the low value is also partly due to the drowning out effect caused by Gramineae pollen. *P. hallii* also shows the same distribution pattern at Harihari (see Chapter 5)

and Lady Lake (see Chapter 7). Apart from Gramineae which contributes 56% of the total, the spectrum provides a good assessment of the relative importance of *Phyllocladus*, *Coprosma* and *Polystichum* in the local vegetation and also accounts for the regional presence of *Nothofagus*. Nevertheless, 3.5% does not indicate that *N. solandri* var. *cliffortioides* is completely dominant in the catchment of Fanghill Stream.

j. WILBFN (*ca.* 580 m): This sample was taken on an old fan surface on the northern side of the Wilberforce River (NZMS 1 S65 897037). *Discaria toumatou* has revegetated the fan with *Poa caespitosa* and amongst these are numerous herbs and small shrubs including *Geranium microphyllum*, *Cotula* spp., *Acaena anserinifolia*, *Oreomyrrhis rigida*, *Anisotome aromatica*, *Hydrocotyle* sp., *Rumex acetosella*, *Viola lyallii*, *Ranunculus lappaceus*, *Cyathodes fraseri*, *Pernettya macrostigma* and *Coprosma rugosa*. The fern *Blechnum penna-marina* was also prominent. The nearest *Nothofagus solandri* var. *cliffortioides* stand is 200 m to the north of the collection point.

Similar trends to those observed in sample KIWIFT from the opposite bank of the Wilberforce River were observed here. Gramineae pollen was again dominant, with a frequency of 56% recorded. Pollen thought to be that of *Discaria* was well represented but this is not surprising considering its local source. Local herbaceous vegetation *viz.* Umbelliferae, *Coprosma*, and monolete fern spores are also well recorded. The one unexpected feature of the spectrum is the near absence of *N. fusca* type pollen. Such low percentages in fossil material would be interpreted by most workers (e.g. McGlone and Topping 1977) as being derived from long distance transport and yet *N. solandri* var.

cliffortioides is a predominant forest type in the Wilberforce Valley. Inconsistencies of this order suggest the need for a detailed long-term trapping survey to be carried out to extend our knowledge of the relative export capabilities of the tree species, at least, and also to give information on the periodicity of flowering of the major wind-pollinated species.

6.4 KELLY RANGE STUDY AREA

6.4.1 Introduction

The Kelly Range forms the southern slope above the Otira River, and terminates at the flood plain of the Taramakau River just northwest of Aickens. Wardle and Hayward (1970) describe the forest and scrub vegetation of the Taramakau catchment in terms of eight associations which have no definite boundaries.

Nothofagus fusca is present in the Taramakau Valley with the main stands upstream from the confluence of the Taramakau and Otira rivers and in the Otehake River catchment where it is found with *N. menziesii* and *N. solandri* var. *cliffortioides*. It is normally associated with *Weinmannia racemosa*, *Quintinia acutifolia* and *Griselinia littoralis*. Scattered stands of *N. fusca* and *N. menziesii* also appear on the northern side of the Taramakau River and on young river terraces. An association of *Metrosideros umbellata* and *Podocarpus hallii* forms a significant proportion of forest cover up to 760 m and is normally combined with *W. racemosa*, *Q. acutifolia* and *Pseudopanax* spp. Above this forest, usually occurring in gullies, is scrub-hardwood of *Hoheria glabrata*, *Griselinia*

littoralis, *Fuchsia excorticata*, *Olearia ilicifolia*, *Myrsine divaricata* and *Aristotelia serrata*. Subalpine scrub of *Dracophyllum longifolium*, *D. traversii*, *Olearia lacunosa* and *Dacrydium biforme* is developed at higher altitudes above which are extensive grasslands of *Chionochloa pallens*, *C. crassiuscula* and on the Kelly Range *C. oreophila* (Evans *et al.* 1969). Broad vegetational units (scrub, forest and grassland) are mapped on Figure 42 which has been redrawn from NZMS 1 S52 (Harper Pass) and S59 (Otira). The locality of the two surface samples is marked on Figure 42.

6.4.2 Vegetation and Pollen Rain at Sampling Sites

a. KR 1: This site lay on a spur top-plateau at about 610 m altitude on the Kelly Range (NZMS 1 S59 102493). The canopy is formed by *Phyllocladus alpinus*, *Dacrydium biforme* and *Libocedrus bidwillii*. The understorey vegetation consists of: *Metrosideros umbellata*, *Elaeocarpus hookerianus*, *Griselinia littoralis*, *Archeria traversii*, *Dracophyllum longifolium*, *Coprosma foetidissima*, *C. astonii*, *Pseudopanax colensoi*, *P. lineare* and *Myrsine divaricata*. The ground is almost completely covered with: *Gahnia procera*, *Libertia pulchella*, *Blechnum minus* and *Hymenophyllum* spp. Downslope towards the west and north *Podocarpus hallii*, *P. ferrugineus*, *Weinmannia racemosa*, *Quintinia acutifolia* and *Nothofagus fusca* occur.

Phyllocladus (62%) was the dominant pollen in the spectrum and is over-represented. The lack of air circulation under the canopy may explain this, and this is especially pronounced with an anemophilous species. *Dacrydium biforme* (6%) was the next most important pollen type but in this instance is under-represented.

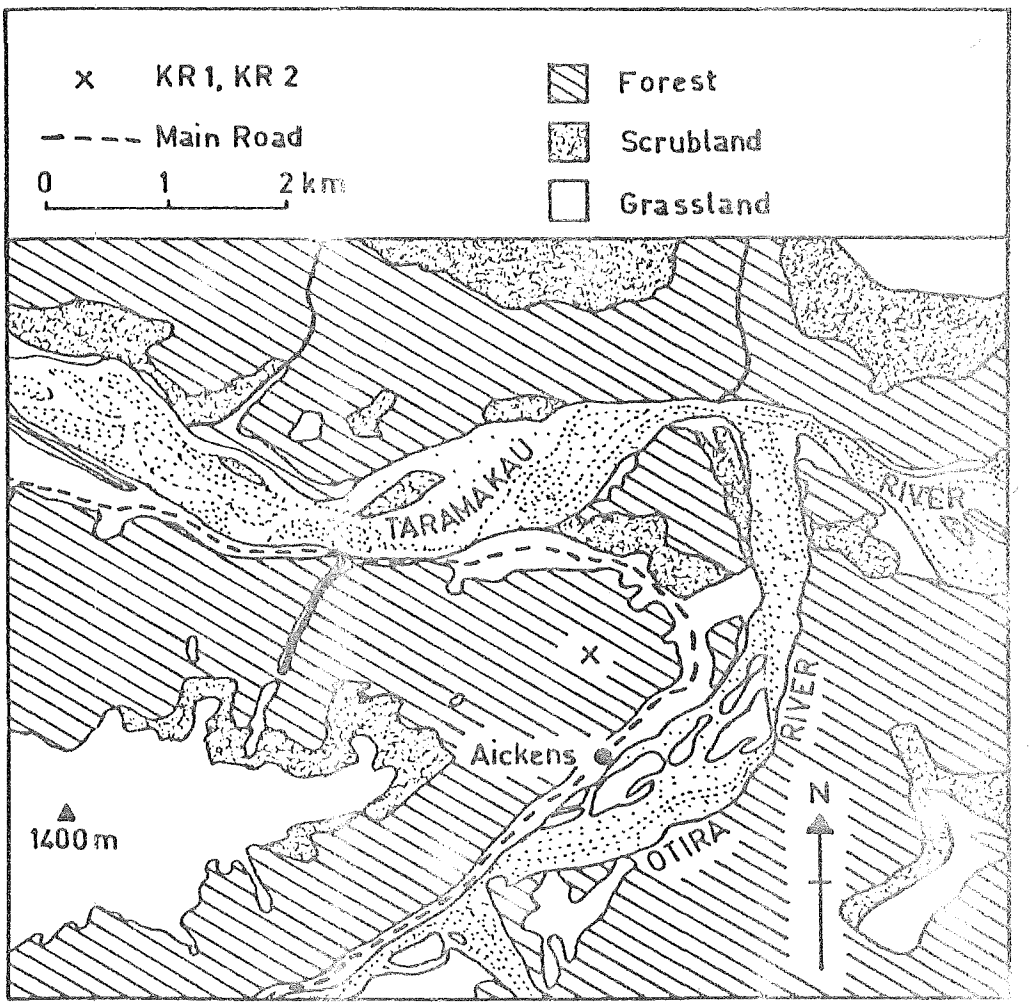


Figure 42. Location of sites on Kelly Range, Westland.

Similarly, *Libocedrus* is scarcely recorded. All other types are recorded in low (<5%) frequencies but these more-or-less reflect their distribution at and in the near vicinity of the collection sites. Transport of pollen into the forest is apparently restricted as shown by the paucity of *Nothofagus fusca* type and Gramineae pollen in the sample. The prevailing wind is westerly and much pollen of these plants would be dispersed up the Taramakau Valley so that which is deposited is substantially "swamped" by the large quantities of *Phyllocladus*.

b. KR 2: The vegetation at this site (50 m east of KR 1) is similar in composition to that at KR 1 but more open. The only additions are *Astelia nervosa*, *Phormium cookianum* and *Cyathea colensoi* in the lower storey.

The major pollen types recorded in KR 1 were also recorded in this sample but their proportions differ. *Phyllocladus* (34%) was again dominant but more correctly represented here as is *Dacrydium biforme* at 13%. *Libocedrus* remained under-represented; it obviously possesses poor relative export. The local abundance of two *Pseudopanax* species has resulted in an 8% frequency. Other major contributors are *Nothofagus fusca* type (6%), perhaps due to the more open nature of the sampling site, *Podocarpus ferrugineus* (4%), *Coprosma* (4%) and Gramineae (5%). *Weinmannia* is under-represented and in this sample shows very limited dispersal of pollen by uplift. This confirms results obtained at Ajax Hill and Meins Knob (this chapter). The regional pollen contribution in this sample is minimal and two major near absentees are *Dacrydium cupressinum* which is widespread in Westland forests and *Nothofagus menziesii* which

occurs less than 1 km from the site. Subalpine scrub and scrub-hardwood components are predominantly absent from the pollen spectrum in both KR 1 and KR 2.

The impression gained from the two Kelly Range samples is that the relative proportions of pollen in the spectra are governed by the influence of local taxa, especially *Phyllocladus*. Little can be ascertained regarding the regional vegetation but percentages such as these might be interpreted as representing a *Phyllocladus-Dacrydium* shrubland which has been recognised by Moar (1971) as being widespread in high country Canterbury immediately following the retreat of the Otiran glaciers.

6.5 MEINS KNOB; UPPER RAKAIA STUDY AREA

6.5.1 Introduction

Meins Knob lies just east of the Main Divide at the head of the Rakaia River at an altitude of *ca.* 1220 m. An account of the flora of the upper Rakaia has been presented by Speight, Cockayne and Laing (1910) and Burrows (1977). The regional vegetation is patchily distributed grassland with isolated stands of tall (>4 m) *Phyllocladus alpinus* scrub. *Nothofagus solandri* var. *cliffortioides* extends some distance up the Rakaia River valley and *N. menziesii* is present in a number of tributaries of the Lake Stream. Figure 43 shows the sparse local vegetation and is redrawn from NZMS 1 S72 (Godley). Sampling site localities are shown on Figure 43.

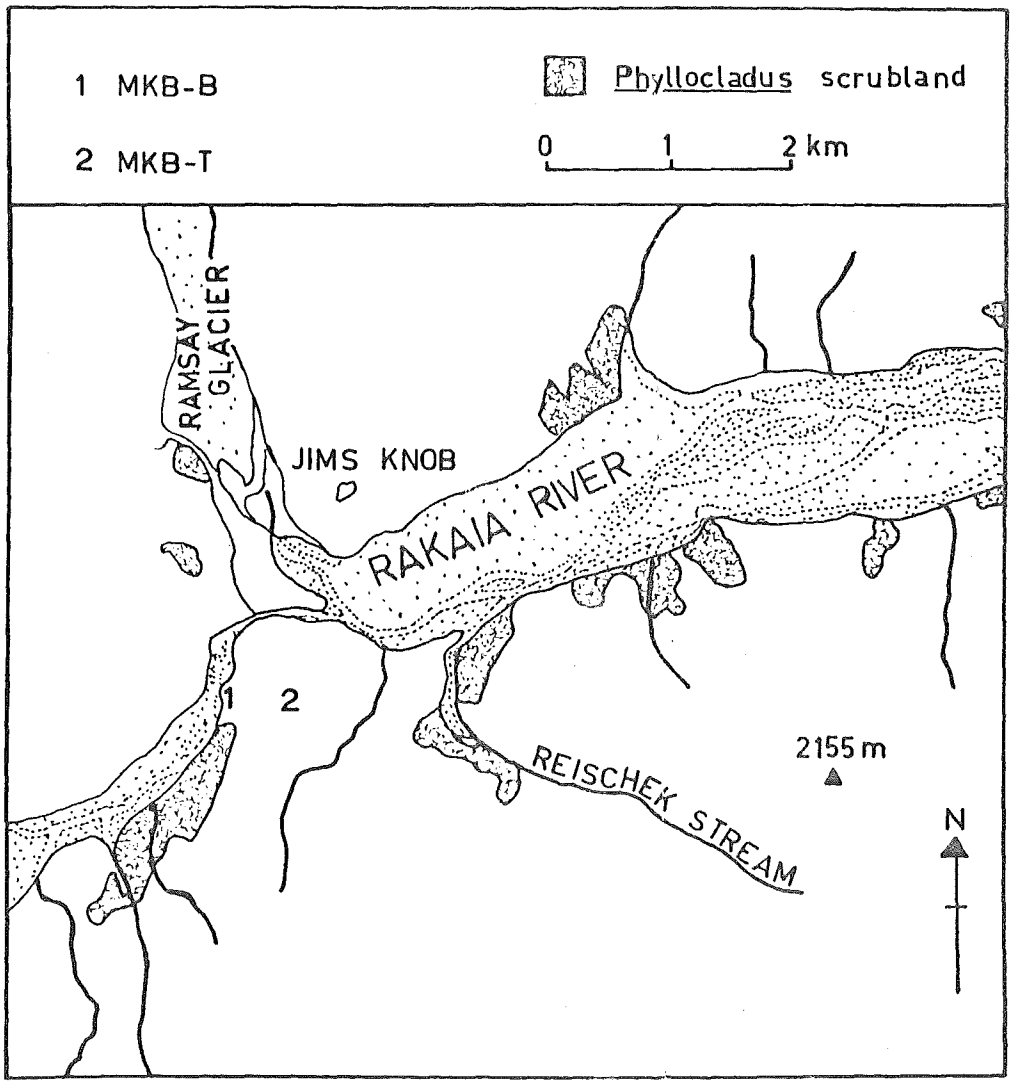


Figure 43. Location of sites at Meins Knob, Upper Rakaia, Canterbury.

6.5.2 Vegetation and Pollen Rain at each sampling site

a. MKB-B: This site lay at the base of Meins Knob (NZMS 1 S72 481855) *ca.* 30 m above the bed of the Rakaia River. In this boggy locality the predominant plants are: *Carex gaudichaudiana, C. echinata, Schoenus pauciflorus, Oreobolus pectinatus, Coprosma pumila, Celmisia glandulosa, Poa colensoi, Anisotome aromatica, Drosera arcturi, Sphagnum fulcatulum* and *S. cristatum.* On the better drained sites adjacent to the bog the following plants are present: *Chionochloa pallens, C. flavescens, Coprosma rugosa, C. ciliata, Dracophyllum uniflorum, D. longifolium, Phormium cookianum, Hebe subalpina, Podocarpus nivalis, Cassinia vauvilliersii, Gaultheria crassa* and *Aciphylla scott-thomsonii. Phyllocladus alpinus* scrub is about 300 m away towards the south-west.

The local and regional vegetation are well represented by four pollen types *viz. Coprosma* (13%), *Phyllocladus* (12.5%), Gramineae (16%) and Cyperaceae (7.5%). Most other local types are poorly represented, including the conifer *Podocarpus nivalis* as previously recorded at MOAST-2. Due to its close proximity to the Main Divide much of the pollen is derived from Westland forests. *Dacrydium cupressinum* (5%) and *Podocarpus ferrugineus* (2%) are consistently recorded but one seemingly anomalous result is a 22% pollen frequency for *Libocedrus.* Such a frequency implies considerable production and dispersal but *Libocedrus* is commonly reputed to have limited pollen export and is consequently poorly represented. Further confusion in interpretation results from its negligible occurrence in MKB-T. *Libocedrus bidwillii* is very important in forests up to 1000 m in Westland forests

(Wardle 1977) and is often emergent so the availability of a source is not a problem. Long-distance transport of *Libocedrus* pollen is often recorded (e.g. Lady Lake, see Chapter 7) but usually only in trace frequencies. *Podocarpus hallii* (which also occurs across the Divide), *Nothofagus fusca* type and *Pinus* pollen are probably derived from further down the valley. The nearest *N. solandri* var. *cliffortioides* forest is 8 km away.

b. MKB-T: This sample was collected at the top of Meins Knob (NZMS 1 S72 485855) in a mixture of grass, *Sphagnum* and sedge vegetation. Those species which are important include: *Chionochloa pallens*, *C. crassiuscula*, *Sphagnum falcatulum*, *S. cristatum*, *Schoenus pauciflorus*, *Carpha alpina*, *Oreobolus pectinatus*, *O. impar*, *Anisotome aromatica*, *A. haastii*, *Coprosma pumila* and *Poa colensoi*.

More or less adjacent are: *Ourisia sessilifolia*, *O. macrocarpa* var. *calycina*, *Celmisia coriacea*, *C. glandulosa*, *C. discolor*, *C. alpina*, *Ranunculus lyallii*, *Hebe macrantha*, *Astelia linearis*, *A. petriei*, *Caltha novae-zelandiae*, *Gentiana bellidifolia*, *Drosera arcturi*, *Gaultheria depressa*, *Cyathodes pumila*, *Phyllachne colensoi*, *Donatia novae-zelandiae*, *Dracophyllum uniflorum* and *Podocarpus nivalis*.

The pollen spectrum is essentially similar to that obtained for the base of Meins Knob except here Cyperaceae pollen (20.5%) is more predominant. Gramineae, *Phyllocladus*, *Coprosma* and Umbelliferae are well recorded, as is the pollen of *Podocarpus hallii* which is perhaps more indicative of its distribution in the upper Rakaia River catchment areas. The local herbaceous vegetation is barely recorded and 1.5% Compositae pollen does not reflect the importance of the

members of this family at and near the site. *Cyathodes* and *Ranunculus* are noted. *Myriophyllum* contributed 6% to the total sum and must have been locally important although it was not recorded on the species list. Greater than 10% of the pollen sum is yielded from Westland with *Dacrydium cupressinum*, *Podocarpus ferrugineus*, *Cyathea smithii* and *Dicksonia squarrosa* present in significant quantities. Pollen of *Weinmannia* and *Metrosideros* are registered in below trace frequencies despite their extensive distribution in forests west of the Main Divide.

6.6 OLD MAN RANGE STUDY AREA

6.6.1 Introduction

The Old Man Range forms the western slope above the Clutha River between Ettrick and Clyde (Mark 1962) with the highest peak, Obelisk at 1680 m. The vegetation has been described by Mark (1962, 1965) and consists of seven vegetation types of which five are tussock grassland, one of semi-desert scab-weed (*Raoulia* spp.) and one of alpine cushion and fell-field. The only forest in the region consists of small, mostly relic, stands of *Nothofagus* forest near the wetter more humid margins. *N. menziesii* extends up to about 640 m near the south-west boundary on the east slope of the Range near Ettrick. *N. solandri* var. *cliffortioides* extends up to 915-1070 m near the north-west in the Shotover and Arrow River catchments and in the north near the Lindis River. A few trees of *N. fusca* and *Podocarpus hallii* occur locally in the Shotover and Arrow River catchments. In the south-west in the upper Waikaia valley there are forests of

N. fusca, *N. menziesii* and *N. solandri* var. *cliffortioides* (Wardle 1970). All three species are present below 700 m but between 700 m and the timberline at 900 m *N. menziesii* alone is present. To the north on the Pisa Range there are stands of *Podocarpus hallii*, with a little *Phyllocladus alpinus*, *Dacrydium bidwillii*, *Dracophyllum longifolium* and locally some *N. menziesii* (Wells 1972).

These surface samples provide a good opportunity to study the extent of pollen transport from a regional source against a probable background of grass pollen only. Their locality is noted on Figure 44 which has been compiled from NZMS 1 S143 (Alexandra) and S152 (Roxburgh).

6.6.2 Vegetation and Pollen Rain at each Sampling Site

a. OMAN S1: The sampling site (NZMS 1 S143 986205) lay at about 1250 m on the Old Man Range north of the Waikaia Valley. The ground conditions were wet and support *Carex gaudichaudiana*, *C. sinclairii*, *Chionochloa rubra* x *rigida*, and the introduced rushes *Juncus effusus*, *J. bufonius* and grasses *Anthoxanthum odoratum* and *Holcus lanatus*. Cushion and turf species include: *Celmisia alpina*, *Oreobolus pectinatus*, *Microtis* sp., *Epilobium brunescens*, *Gnaphalium mackayi*, *Ranunculus* sp., *Oreomyrrhis colensoi*, *Plantago novae-zelandiae*, *Juncus novae-zelandiae*, *Hydrocotyle* sp. and *Cerastium* sp.

The pollen spectrum is dominated by Gramineae (48%) and *Nothofagus fusca* type (25%). The latter is in accordance with McKellar (1973) who found that *N. fusca* type pollen is better dispersed than *N. menziesii* pollen. Here the values of *N. menziesii* were only as high as 4%. Apart from Gramineae

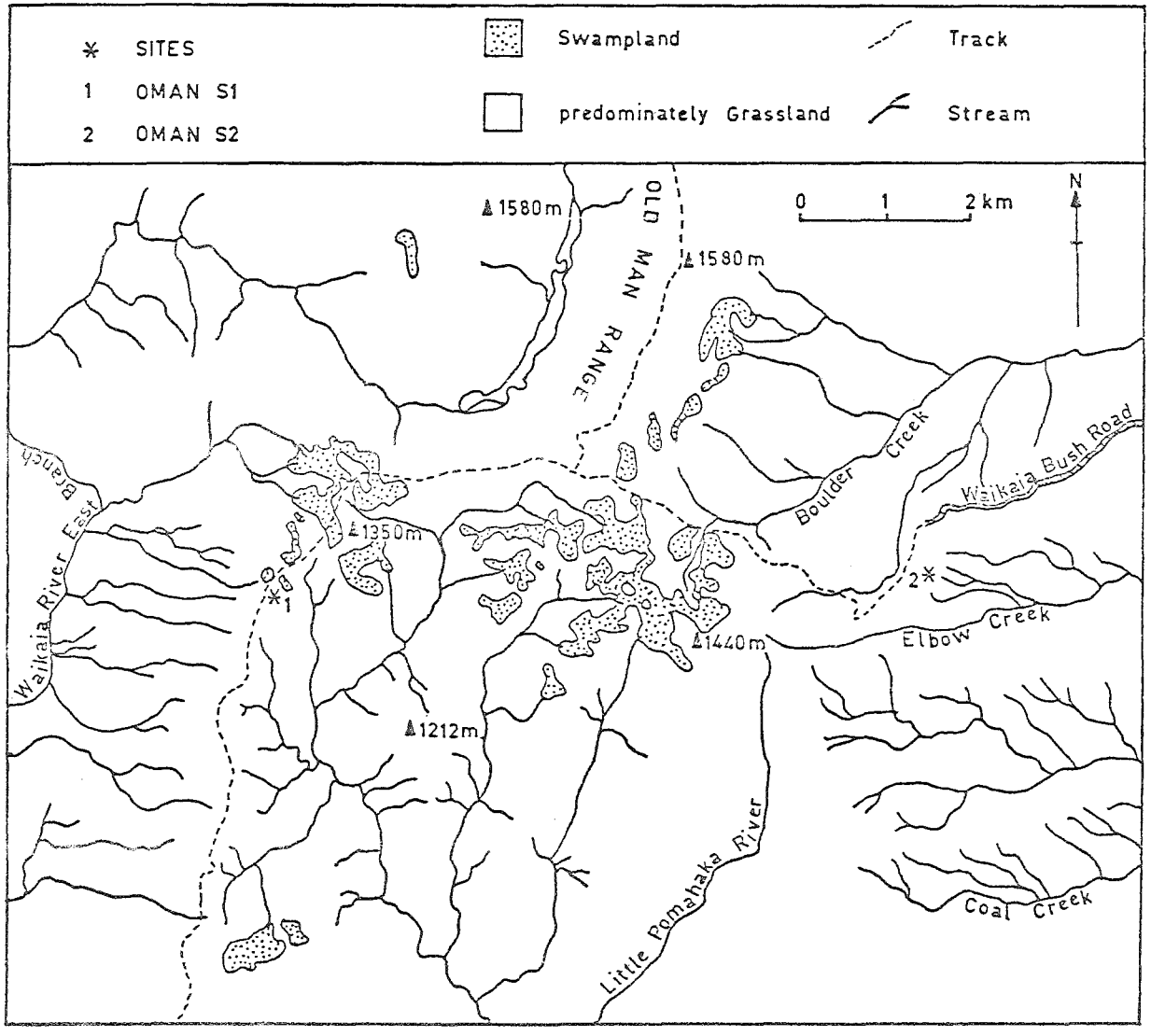


Figure 44. Location of sites on the Old Man Range, Otago.

the local plants provide very little of the total pollen and Cyperaceae is considered here to be under-represented. *Pinus* pollen contributed 6% and *Podocarpus hallii* 1%, but in the latter instance this is not surprising since *P. hallii* is widespread (Wells 1972) and would have a fragmentary pollen output.

b. OMAN S2: *Hebe odora* and *Chionochloa rigida* are the major components of the vegetation at this site stationed at about 1100 m on the eastern side of the Old Man Range (NZMS 1 S143 074207) near the Waikaia Bush Road. The township of Roxburgh is southeast of the sampling site. Other plants around the site are: *Celmisia coriacea, C. sessilifolia, C. alpina, C. lyallii, Dracophyllum muscoides, Hebe* cf. *lycopodioides, Poa colensoi, Rumex acetosella, Gentiana bellidifolia, Cyathodes pumila, Pentachondra pumila, Aciphylla hectori, Coprosma pumila, Gaultheria depressa, Gnaphalium mackayi, Luzula rufa, Agrostis subulata, Carex kirkii, Phyllachne colensoi, Drapetes lyallii, Oreobolus gaudichaudiana, Epilobium alsinoides, E. brunnescens, Drosera arcturi, Schoenus pauciflorus* and *Lycopodium fastigiatum.*

Gramineae pollen (61%) is the dominant component but the spectrum does not adequately reflect the vegetation from which the sample was taken. *Taraxacum* type pollen contributed 12%, and *Rumex* is well recorded. Cyperaceae, Umbelliferae, *Coprosma, Drapetes* and *Hebe* are present in low frequencies and barely reflect their local importance, while *Nothofagus fusca* type and *Pinus* (both <3%) and *Phyllocladus* (1%) signify transport from a distant source. *Casuarina* pollen which has good relative export (Moar 1969; Dodson 1975) was noted; it may have originated in Australia but is more likely to have come from plants somewhere in the region.

6.7 STEWART ISLAND

6.7.1 Introduction

Stewart Island lies approximately 30 km south of mainland New Zealand. In the north is a high ridge which culminates in the highest peak (Mt Anglem) at 980 m. South is the flat valley of the Freshwater River which is separated from the Rakeahua Valley by Mt Rakeahua, at an altitude of 675 m. The Tin Range, containing the summits of Mt Allan (750 m) and Table Hill (716 m), extends along the centre of the Island from the Rakeahua Valley to the coast at Port Pegasus. To the west of the Freshwater River is a wide flat area of grassland separated from Mason Bay by sand dunes.

Cockayne (1909) provided the first description of the vegetation of Stewart Island and recent work (Wells and Mark 1966; Evans and Fine 1976; Williamson 1976; Ross 1977) has provided detailed analyses of selected areas of the island.

The predominant vegetation association is forest of *Dacrydium cupressinum*, *Podocarpus ferrugineus*, *Metrosideros umbellata* and *Weinmannia racemosa*. This ascends to around 460 m at which point the forest gives way to a belt of *Leptospermum scoparium* with *Dacrydium biforme* (on Mt Anglem) and then to true sub-alpine scrub with *Olearia colensoi* dominant on those mountains which exceed 500 m. *Dacrydium intermedium* does not extend northwards beyond the Freshwater Valley but is important in areas of wet ground or in situations exposed to the wind. *Podocarpus hallii* occupies the clay sites.

Nearshore the forest merges into coastal scrub with

Senecio reinoldii and *Olearia colensoi* var. *grandis* the major components. Above the subalpine scrub zone on the higher peaks there are tussock grasslands of *Chionochloa pungens* and, especially on Mt Anglem, *C. flavescens*.

Figure 45 shows the locations of the surface samples.

6.7.2 Vegetation and Pollen Rain at each Sampling Site

a. Mount Rakeahua: This site lay in an exposed situation at about 520 m, below the summit and on the south-east side of Mt Rakeahua (NZMS 219 909356). The local ground conditions support a cushion bog community surrounded by some low scrub of *Olearia colensoi* and *Leptospermum scoparium*, *Chionochloa pungens*, *Celmisia linearis*, *Mitrasacme novae-zelandiae* and *Aciphylla traillii*. Cushion plants include *Donatia novae-zelandiae* *Oreobolus pectinatus*, *Gaimardia setacea* and *Dracophyllum politum*.

The principal components of the pollen spectrum are *Dacrydium cupressinum* (26%), *Podocarpus ferrugineus* (12%), *Nothofagus fusca* type (9%), *Leptospermum* (7%) and Gramineae (7%). This provides a good estimate of the relative abundance of these groups on Stewart Island with the exception of *N. fusca* which originates mainly from Southland and Fiordland forests and thus exhibits excellent long distance dispersal. The frequencies for *D. cupressinum* and *P. ferrugineus* are almost certainly supplemented from extensive stands of these two species on Codfish Island (Fineran 1966) which is directly in the path of the prevailing westerly. Two notable appearances from the mainland are *N. menziesii* and *Libocedrus*, the former is common in Southland while it is difficult to assess the 3% pollen frequency of the latter which would

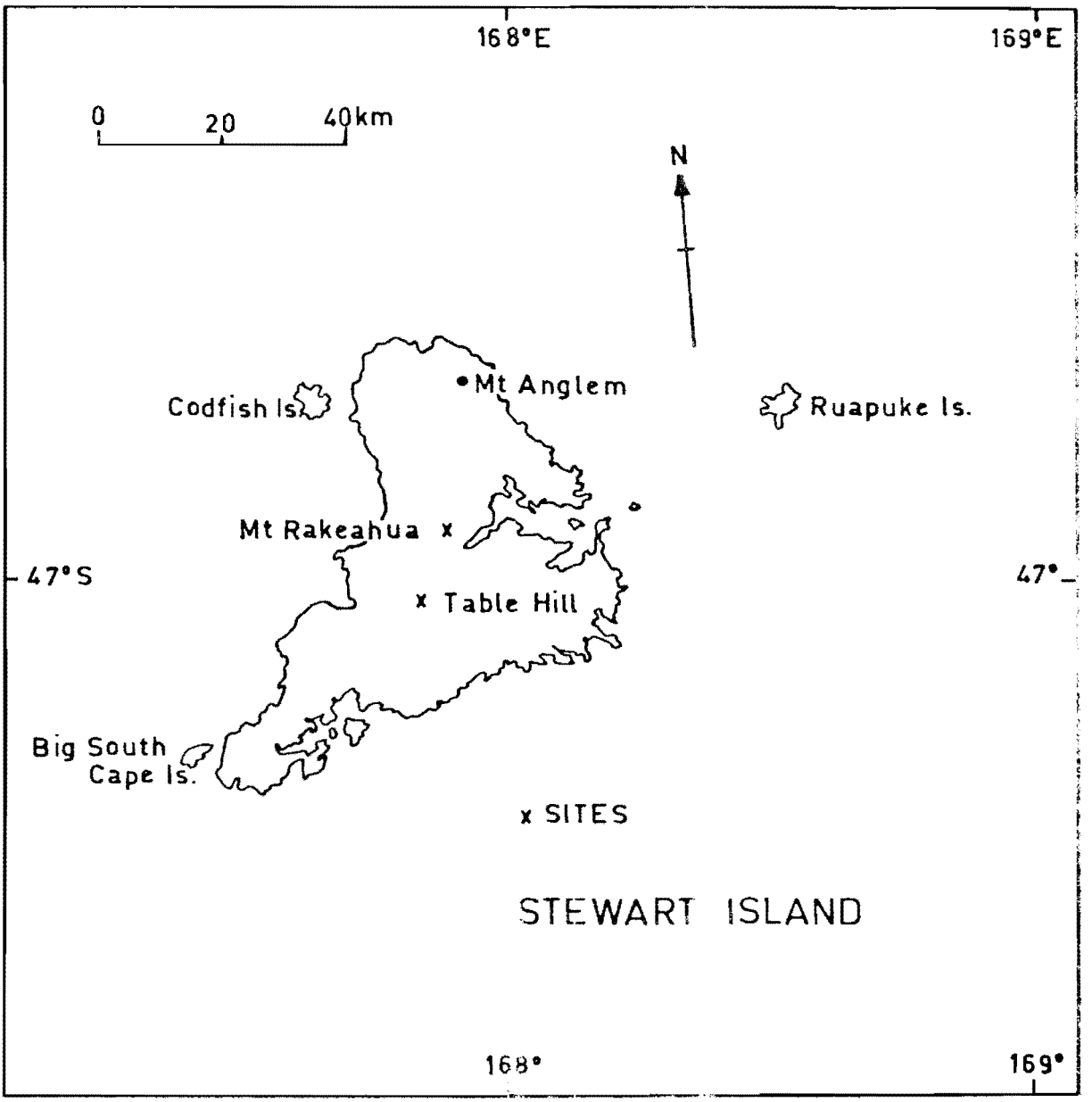


Figure 45. Location of sites on Stewart Island, New Zealand.

have its nearest source in Central Otago. Previous observations with *Libocedrus* pollen suggest that stands of *Cupressus* grown as shelter belts in farmland in Southland may be responsible for some of the recorded figure. Most pollen of the Cupressaceae is difficult to distinguish below the generic level.

The understorey species prominent in the forests at lower altitudes are recorded in low frequencies. Components of the local bog vegetation are low pollen producers and are infrequently recorded.

b. Table Hill: At this site (NZMS 219 906203), on the summit of Table Hill (716 m) the vegetation is dominated by cushion plants similar to those at Mt Rakeahua. Surrounding the site are *Olearia colensoi*, *Senecio lyallii*, *Dracophyllum politum*, *Aciphylla traillii*, *Astelia linearis*, *Chionochloa pungens* and *Anisotome aromatica*.

The local bog and surrounding vegetation are poorly represented apart from Compositae and Umbelliferae, whose representatives contribute 10% to the total. The spectrum is dominated by regional pollen derived from updrafts from lower altitudes and is documented elsewhere (e.g. Moar 1970, Fox Range). *Nothofagus fusca* (16%) far exceeds its actual presence and does not signify derivation from a long distant source. *Dacrydium intermedium* type pollen is adequately accounted for but *Weinmannia* and *Metrosideros* are under-represented.

6.8 DISCUSSION AND CONCLUSIONS

Conclusions drawn from analyses of pollen spectra in surface samples assist in our knowledge of the dispersal and thus representation characteristics of New Zealand floral elements. These can now be utilised in providing local and perhaps even widespread solutions to problems encountered in understanding results of fossil pollen analysis. Estimates of the representations and pollination mechanism (based on Thomson 1927; Heine 1937; Faegri and van der Pijl 1971) of all plants encountered in this thesis are given in Table 9 (general summary). The order of the pollen types in the table is the same as has been applied in Appendix I.

Pollen representation at all sampling sites is shown not to be in the order of source species proportion in the vegetation. Various explanations can be cited for such a phenomenon, the magnitude to which these apply is largely unknown.

i. The pollen output of individual taxa, and the periodicity of flowering are pertinent when considering surface samples of comparatively recent age. The mode of pollination usually determines pollen production such that wind-pollinated (anemophilous) plants need to produce large numbers of well travelled pollen grains to be successful compared to those with animal oriented (entomophilous) pollination mechanisms. The gymnosperms, some Dicotyledons (e.g. *Coprosma*, *Ascarina*), Gramineae, Cyperaceae and Pteridophytes in the New Zealand flora are anemophilous while most others are entomophilous.

ii. Dispersal distances of individual grains vary between taxa and are controlled by aerodynamic character-

istics of the grains, topography, vegetation cover and structure, meteorological conditions and the height of the source. *Podocarpus nivalis* is a high pollen producer and yet it is poorly represented, seemingly due to its low prostrate stature.

The absence of local vegetation or the presence of low pollen producers in the local vegetation around the site (e.g. cushion bogs on Ajax Hill, Old Man Range and Stewart Island) is reliably indicated by the accentuation of percentages of pollen types known to represent a long-distance transported component. Also, as indicated by the samples from higher altitudes analysed in this thesis, several wind dispersed pollen and spore types are recorded in high frequencies upslope of the source e.g. *Dacrydium cupressinum*, *Podocarpus ferrugineus*, *P. spicatus*, *Cyathea smithii* and *Dicksonia squarrosa*. Over-represented pollen types (especially those known to be ineffectively dispersed, e.g. *Muehlenbeckia*, *Raoulia*) are valuable indicators of a nearby source as are rare appearances which more than likely signify *in situ* occurrence, e.g. *Epilobium*, *Drapetes*. Overall it is almost impossible to distinguish one vegetation formation from another at the level of pollen identification; especially with *Nothofagus fusca* type, Gramineae and Compositae where there is a complex of source types.

iii. Differential pollen preservation will have a marked effect on representation. Little is known from New Zealand pollen studies of relative preservation of pollen types but such a force must be acting and it is possible that under-represented wind pollinated taxa (e.g. *Libocedrus*, *Dacrycarpus*) are poorly preserved in surface samples

where these are subjected to oxidative processes.

iv The area of vegetation effectively recorded in any pollen assembly is determined by the extent to which the regionally derived "background" pollen is diluted by locally produced pollen. In this respect the nature of the sampling site is important. An open site with low vegetation may promote the occurrences of pollen derived by airborne pollen transport from outside the area, while a closed site (e.g. any forest sample) registers little background pollen due to restricted movement under the canopy and a high trunk space component (see Tauber 1977). Numerous examples of each situation are presented in this thesis.

The frequency of occurrence of any pollen or spore type in a surface pollen spectrum is likely to be determined by the mobility of that type, and by the pollen source strength - source distance relationships of other pollen and spore types with which it is growing. Consideration must be made of these factors when interpreting floral history from pollen diagrams and with so many pollen types being rarely encountered in above trace frequencies it is easy to form a false picture of the vegetation at the site of deposition.

CHAPTER 7

MODERN POLLEN RAIN FROM LADY LAKE, NORTH WESTLAND

7.1 INTRODUCTION

Analysis of data obtained from lake sediments not only has to take into account the production and dispersal of pollen grains from the vegetation in the vicinity of the lake but must also consider the behavioural characteristics of the pollen grain on and in the water. The deposition of pollen grains in lake sediments is governed by factors of sedimentary control (Twenhofel and McKelvey 1941, p. 827).

Moar (1970a) and Dodson (1976) demonstrated that moss cushions show great variability in pollen frequencies of particular species due mostly to local presence, absence and abundance of source plants. Others (e.g. Anderson 1973) have noted that differential production of tree species causes changes in tree pollen spectra over short distances. Although no work has been completed in New Zealand, variability has been shown to exist in pollen spectra from lake surface sediments elsewhere (e.g. Davis, Brewster and Sutherland 1969). Hopkins (1950) observed differential flotation and deposition of coniferous pollen grains compared to pollen of other tree taxa. Deciduous tree pollen sunk rapidly compared with the bladder equipped conifer grains which tended to float. The pattern of distribution of pollen involves preferential sedimentation of small grains (Davis, Brubaker and Beiswenger 1971), as well as conifer grains

with bladders, in shallow water, which leads to higher ratios of such taxa with respect to the rest of the pollen in these sediment locations. The presence of a local source is normally reflected in high frequencies in the adjacent sediment. Davis and Brubaker (1973) note the occurrence of preferential deposition which distorts the original ratios in which pollen enters the lake from the air causing variations in the pollen percentages in sediment from different parts of the basin. Water circulation may also result in the deposition of pollen grains with slow sinking speeds into the epilimnion sediments.

Other factors causing variability in lake sediment spectra are the mixing of sediments by organisms dwelling in the lake and differential degradation and corrosion of pollen. R.B. Davis (1967) suggests that mixing of the sediments takes place *via* sediment ingesting burrowing organisms and certain kinds of fish which feed heavily on mud dwelling benthos. However, he notes that if mixing only affects the sediment deposited during a few years, it may well be advantageous in that it integrates years of high and low pollen production thus producing a seemingly homogeneous sample. Sangster and Dale (1961, 1964), Havinga (1964, 1967) and Birks (1970) report pollen deterioration in lake and bog sediments and conclude that differential preservation may cause differences in the representation of certain pollen types e.g. *Acer* became almost unrecognisable after two years which would no doubt result in a misinterpretation of its history from the fossil record. Pond and lake sediments tend to be more destructive than *Sphagnum* bog implying that bog sediments are probably more desirable for a study of

vegetation history thus minimising the influence of corrosion.

Nevertheless, some lakes show only small variation in the percentages of the different pollen types in sediments from equivalent depths. Davis (1968) attributes this to seasonal water circulation resulting in initial resuspension of the top few centimetres of sediment and then redeposition in all parts of the lake basin. Thermal stratification may also be instrumental in reducing variation in pollen percentages in lake sediments. Janssen (1973) demonstrated that in a medium sized lake away from the direct influence of local sources, pollen types in the assemblage are present in roughly constant proportions. This he explained by regional pollen deposition.

7.2 STUDY METHODS

At Lady Lake, North Westland, moss cushions and lake sediments were analysed for their pollen content. The collection of surface muds was as described in Chapter 3.

The pollen rain from lake sediments are compared to basal area data for the major vegetation types derived from data obtained by Drake (1977).* It is therefore possible to make a comparison between lake sediments and moss cushions as collectors of modern pollen rain.

7.3 DESCRIPTION OF THE STUDY AREA

Lady Lake (NZMS 1 S52 066697) is 4 km north of Rotomanu and 7.5 km west-northwest of Moana (Figure 46).

*See Drake for full species lists.

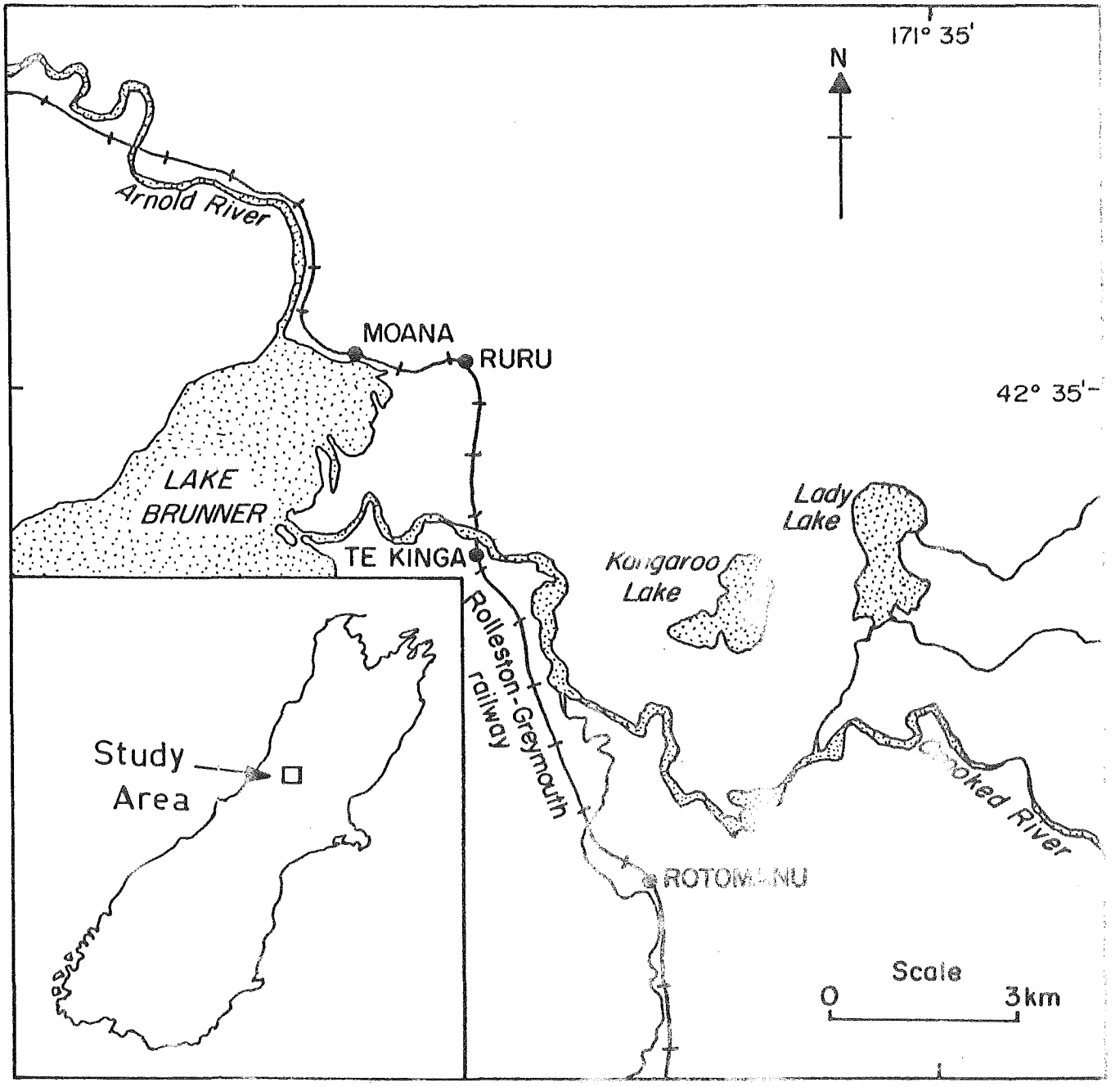


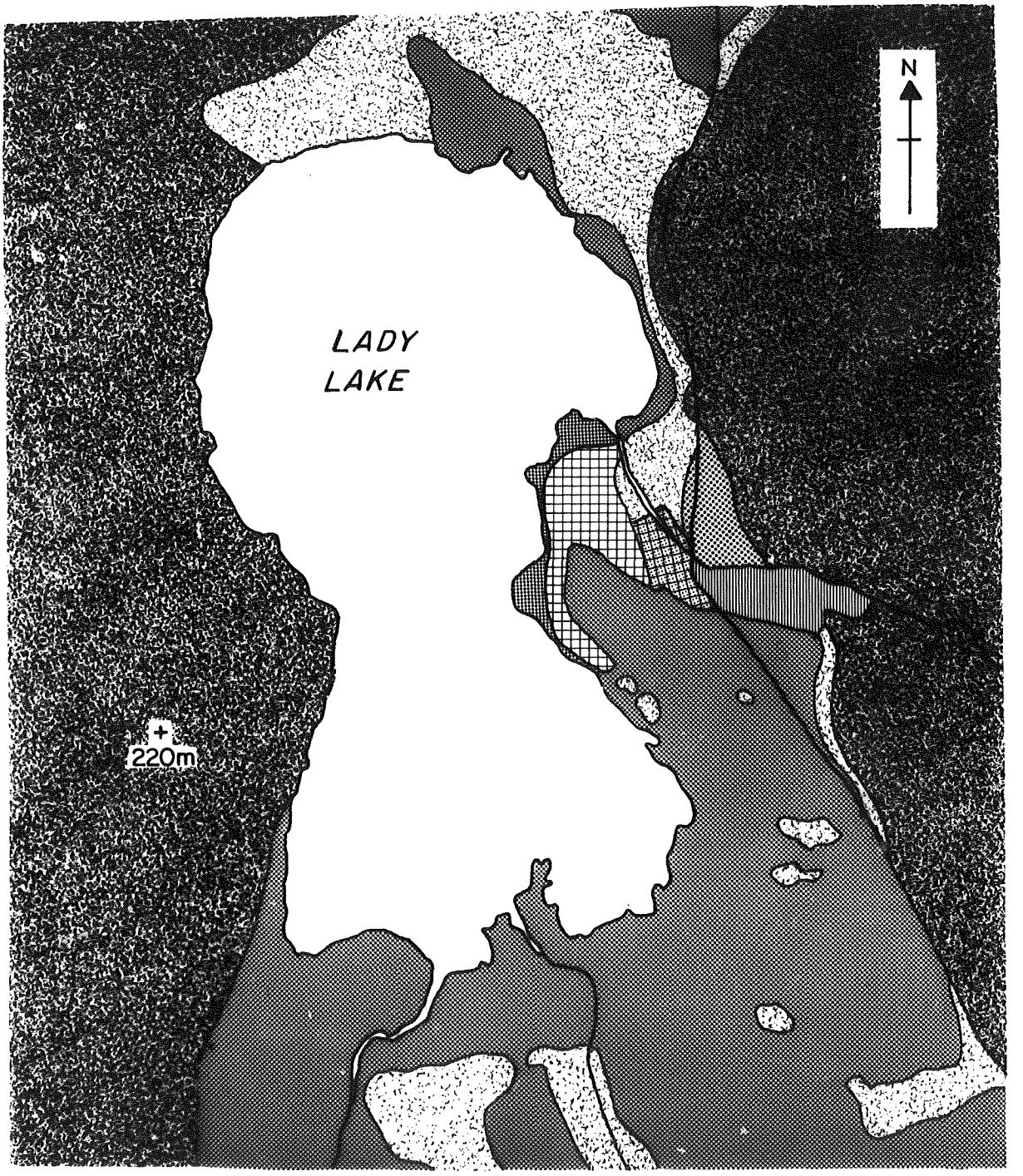
Figure 46. Location of Lady Lake, North Westland.
Inset: South Island giving general
locality of study area.

The lake surface is 107 m above sea level and approximately 1.75 km^2 in extent (Drake 1977). The lake formed between the moraine of the Kumara-3 ice advance (Suggate 1965) and recent alluvial gravels. Water enters the lake *via* many small creeks, including Sam Creek and Rough and Tumble Creek (Figure 52), *via* seepage, especially from the east and west sides, and *via* the precipitation of 3432 mm yr^{-1} (New Zealand Meteorological Bulletin 1974). Lady Lake Creek regulates water level by overflow into Crooked River. No data on lake levels is available for Lady Lake but Lake Brunner, some 10 km to the west, is known to fluctuate up to 4 m (data supplied by New Zealand Hydrological Survey) after periods of heavy rain.

7.4 VEGETATION SURROUNDING LADY LAKE

The vegetation (Drake 1977) consists of mixed forest, swamp communities and cleared areas (Figure 47). To the north, south, and east, the lake is bounded by swampland dominated by *Phormium tenax*, *Leptocarpus similis*, *Carex* spp., *Coprosma tenuicaulis*, *C. propinqua* and *Leptospermum scoparium* (Figures 48, 49, 51). Beyond this swampland to the north there is a band of *Dacrycarpus dacrydioides* and to the east and west are extensive tracts of mixed podocarp/hardwood forest (Figure 50). The latter contains *Dacrydium cupressinum*, *Weinmannia racemosa*, *Quintinia acutifolia*, *Podocarpus ferrugineus*, *Carpodetus serratus*, *Elaeocarpus dentatus* and *E. hookerianus* with an open understorey. Ground cover consists mainly of *Blechnum*, *Asplenium* and *Hymenophyllum* species, but the lianes *Metrosideros perforata* and *M. diffusa* are also present. Vegetation within the lake is sparse and only *Elodea canadensis*, *Myriophyllum* sp.,

Figure 47. Vegetation map of area surrounding Lady Lake. Redrawn, with permission, from Drake (1977).


N
LADY
LAKE
220m
podocarp/hardwood
Dacrycarpus
swamp vegetation
Aristotelia/Fuchsia
Pteridium esculentum/Swamp vegetation
Coprosma spp/Pennantia/Coriaria
Dacrycarpus/Podocarpus/Dacrydium cupressinum
250m

Potamogeton ochreatus, *Typha orientalis*, *Eleocharis spacelata* and *Juncus* spp. were recorded. Algae are also few in number (Jolly and Brown 1975) due, in part, to highly leached soils and to the surrounding organic soil making plant nutrients less readily available. Pasture is found to the north and south of Lady Lake beyond the forested areas.

7.5 LADY LAKE SURFACE SAMPLES

Figure 52 shows the locations of six moss and nine lake sediment surface samples in the Lady Lake basin. The pollen percentages, based on a pollen sum of total pollen and spores, are presented in Figure 53. Figure 54 compares pollen percentages in the lake samples with basal area percentages (from Drake 1977) for the major tree species recorded in the vegetation surrounding the lake. The lake samples in both figures are arranged in order of increasing water depth.

7.5.1 Vegetation and Pollen Rain at Forest Sampling Sites

a. PHa, PHb, PHc - podocarp/hardwood forest: PHa was collected within *Podocarpus ferrugineus - Quintinia acutifolia* forest. There is a sparse understorey of *Dicksonia squarrosa* and *Myrsine salicina* and ground cover includes species of *Metrosideros*, *Blechnum* and *Asplenium*. The second sample PHb was collected about 30 m from PHa and the main canopy trees are *Dacrydium cupressinum*, *Podocarpus ferrugineus*, *Weinmannia racemosa*, *Quintinia acutifolia* and *Pseudowintera colorata*, *Metrosideros perforata*, *Gleichenia cunninghamii*, *Blechnum* spp. and *Asplenium* species dominate the mid

Figure 48. *Dacrycarpus dacrydioides* and swamp vegetation of *Carex* species and *Phormium tenax* at the mouth of Sam Creek.

Figure 49. Swamp vegetation of sedges and *Coprosma* species on the eastern margin of the lake. The core sample described in Chapter 8 was collected in this vicinity.

to lower storey. Sample PHc was collected 25 m and 55 m south of PHb and PHa respectively. The vegetation is similar to that at PHb except for the addition of *Myrsine salicina* and a reduction in the ground cover to levels below 20%.

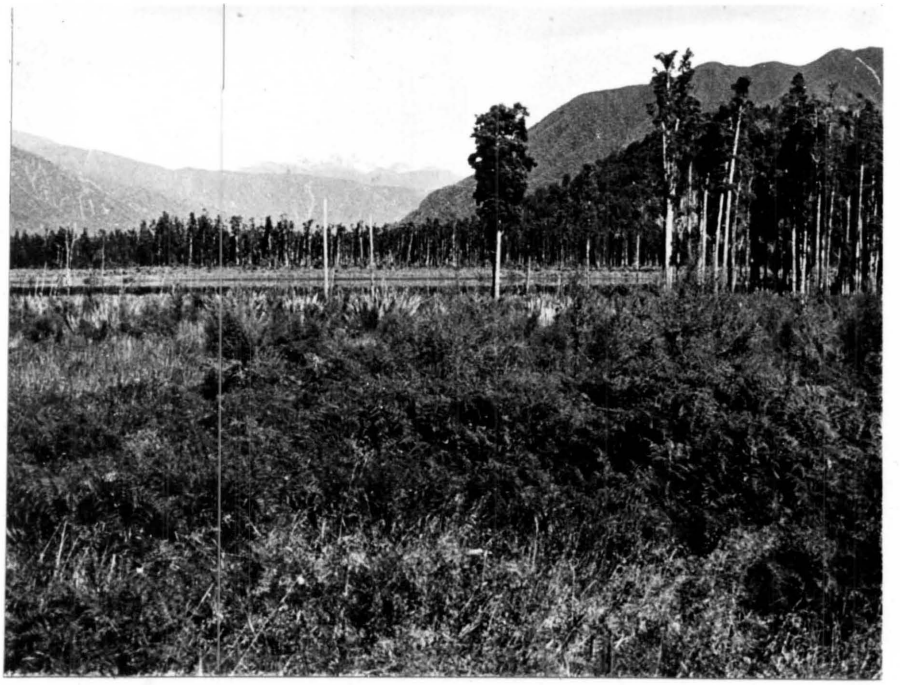
Pollen of *Weinmannia*, *Dacrydium cupressinum* and *Quintinia* dominate all three samples (Figure 53). Sample PHb had a 30% pollen frequency for *Quintinia* which suggests the close proximity of a source(s) to the sample. *Podocarpus ferrugineus* and the understorey species *Myrsine salicina* and *Dicksonia squarrosa* are poorly represented. The tree fern *Cyathea smithii* contributes 17% of the total pollen and spore spectrum at PHa. This indicates good relative export from outside the immediate sampling area. Grass pollen contributes consistently more than 5% of the total pollen at all three sites, no doubt derived from the extensive areas of farmland to the north and south of the lake (grasses were not observed in the vegetation at the sampling sites).

b. DDd - *Dacrycarpus dacrydioides*-podocarp/hardwood transition: This site lies between a wetland forest dominated by *Dacrycarpus dacrydioides* and the podocarp/hardwood type association described for sites PHa-c. Hardwoods are limited in extent because of seasonal flooding but isolated individuals of *Weinmannia racemosa*, *Quintinia acutifolia*, *Aristotelia serrata*, *Pseudowintera colorata*, *Neomyrtus pedunculata*, *Elaeocarpus hookerianus*, *E. dentatus*, *Pseudopanax crassifolius* and *Coprosma* spp. are present. *Dicksonia squarrosa* is present on raised mounds where *Metrosideros perforata* and sedges form the ground cover.

The pollen spectrum is dominated by *Dacrydium cupressinum* and sedge pollen. *Podocarpus ferrugineus*, *Coprosma*, *Weinmannia*

Figure 50. Looking across Lady Lake to the podocarp/ hardwood vegetation which predominates along the western margin.

Figure 51. *Dacrycarpus dacrydioides* in the background and *Pteridium esculentum* in the foreground at the southern end of Lady Lake.



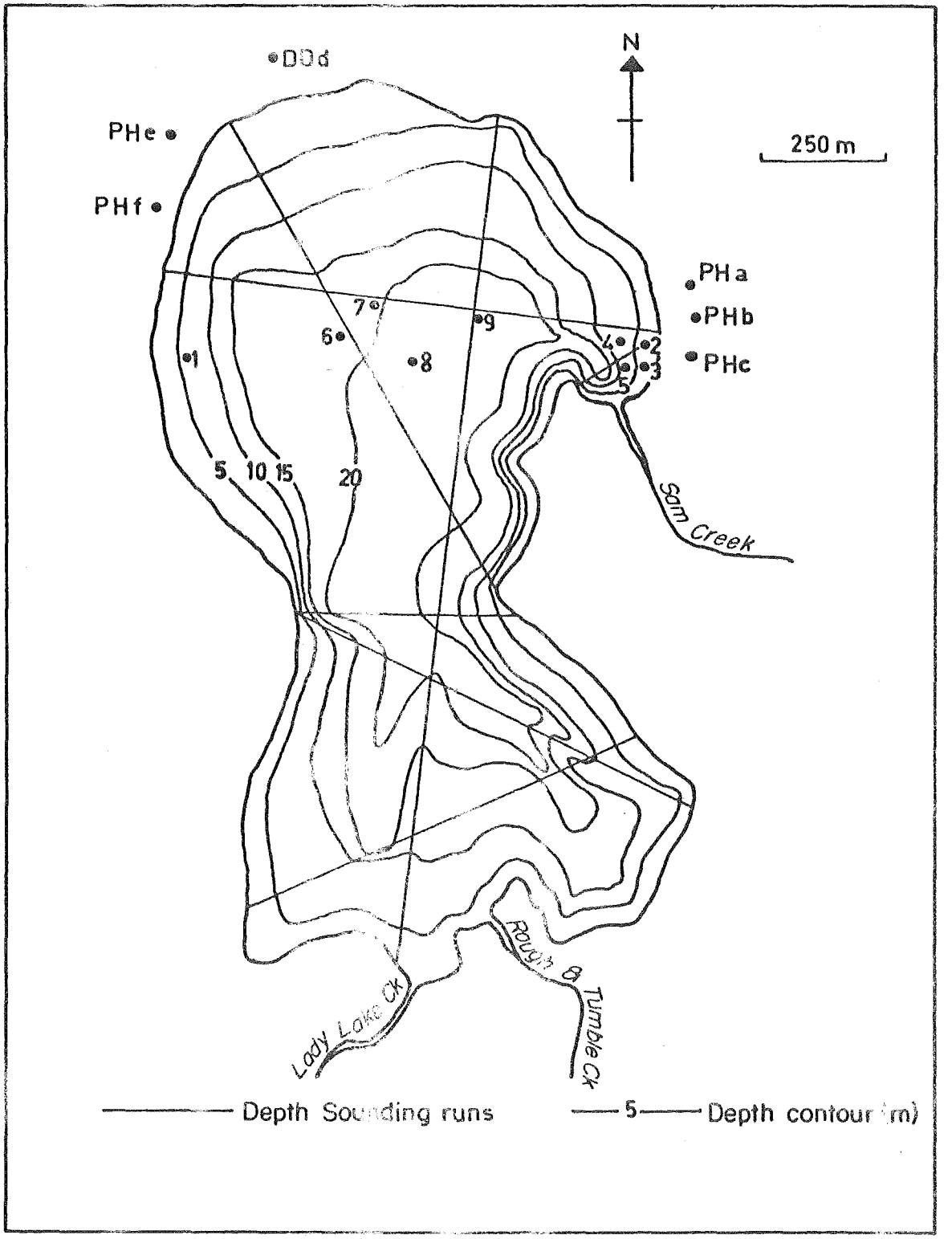


Figure 52. Location of moss and lake sediment samples at Lady Lake.

racemosa and *Dicksonia squarrosa* are well represented to the exclusion of *Dacrycarpus dacrydioides*. *Nothofagus fusca* type pollen accounts for over 5% of the total pollen and doubtless originated from its nearest sources 8 km to the north-east in the Hochstetter State Forest, and to a small stand of *N. fusca* just north of the lake (S.R. June, pers. comm.).

c. PHe, PHf - Podocarp/hardwood forest: Although similar to the forest near samples PHa-c, its structure is altered because of human disturbance. Isolated individuals of *Dacrydium cupressinum*, *Podocarpus ferrugineus* and *P. hallii* form the upper canopy below which is *Quintinia acutifolia* and *Weinmannia racemosa*. At lower levels *Phyllocladus alpinus* (especially near the lake edge), *Myrsine salicina*, *Pseudopanax crassifolius*, *Metrosideros perforata* and *Gleichenia cunninghamii* occur. This composition is reflected more-or-less proportionately in the pollen spectra with the exception of *Myrsine* and *Gleichenia* which are under-represented.

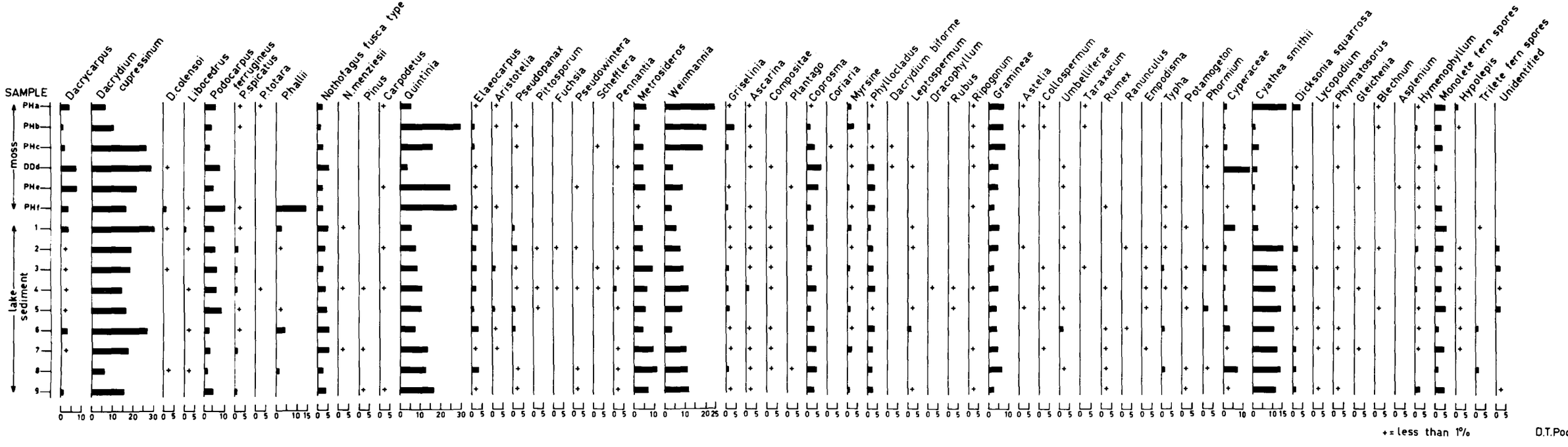
7.5.2 Lake Surface Sediment Analysis

The major pollen types recorded in the lake sediment samples are all derived locally. These include *Dacrydium cupressinum*, *Quintinia*, *Weinmannia*, *Cyathea smithii*, *Elaeocarpus*, *Metrosideros*, *Myrsine*, *Griselinia*, *Podocarpus ferrugineus*, *Coprosma*, *Nothofagus fusca* type, Gramineae and monolete fern spores. Most of these types are favourably represented when compared to their representation in the local vegetation (Figure 54), the major exceptions being *Weinmannia* which is under-represented and *Cyathea* and *Metrosideros* which are over-represented. *Dacrycarpus*, *Carpodetus*, *Phormium tenax* and the

Figure 53. Pollen diagram for Lady Lake surface samples. Sediment samples are arranged in order of increasing water depth.

MODERN POLLEN RAIN, LADY LAKE, WESTLAND

Pollen Sum: Total pollen and spores



+ = less than 1%

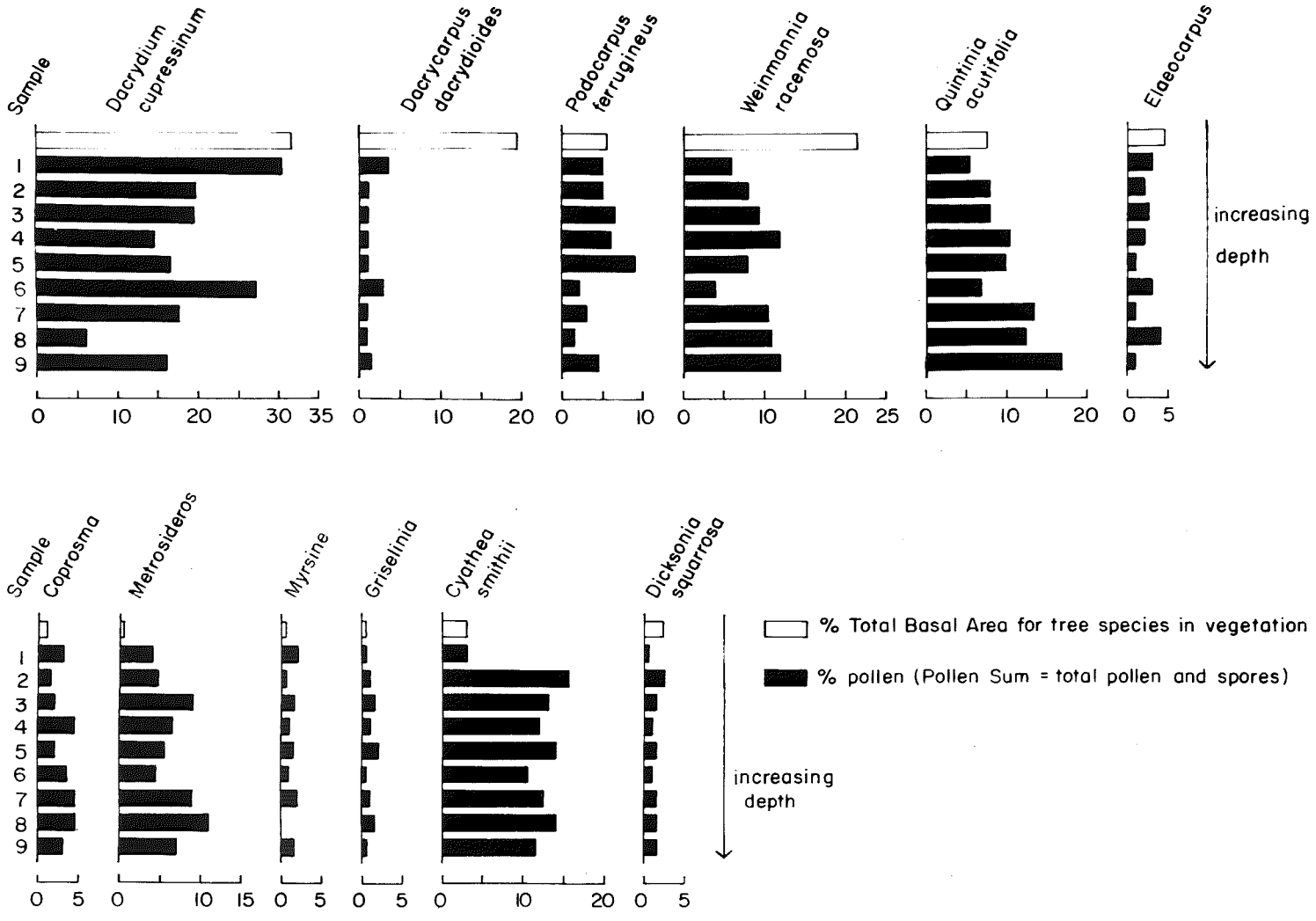
D.T.Pocknall 1977

sedges are all under-represented. The occasional appearance of *Dacrydium biforme*, *Nothofagus menziesii*, *Dracophyllum*, *Libocedrus*, Umbelliferae, Compositae and *Collospermum* is explained by long distance transportation from Granite Hill in the south-east and Bell Hill in the north-east where these taxa are found.

7.6 DISCUSSION

Pollen derived from locally growing trees are the major components of modern pollen spectra derived from Lady Lake samples (Figures 53, 54). This is attributable to the relatively small surface area of the lake and the presence of forest vegetation at the lake margins for at least two-thirds of the lake perimeter. Transport from outside these areas is relatively small. Comparison of the pollen frequencies of tree species in the local vegetation with their basal area percentages (Figure 54) reveal quantitative relations similar to those shown in the study in South Westland (see Chapter 5). The salient features are the over-representation of *Cyathea smithii*, *Quintinia* and *Metrosideros*, the proportionate representation of *Dacrydium cupressinum* and *Dicksonia squarrosa* and the under-representation of *Dacrycarpus* and *Weinmannia*. Of special importance, and contrary to previous work, is the more-or-less proportionate representation of *Podocarpus ferrugineus* and *Elaeocarpus*. Perhaps there is no masking by local dominants at the lake margin (see discussion Chapter 5). The over-representation of *Metrosideros* is a consequence of the importance of the lianes *M. perforata* and *M. diffusa* which provide pollen but are under-represented in basal area analyses.

Figure 54. Relationship between pollen rain and forest composition for main tree types recorded in lake sediment, Lady Lake, North Westland. The samples are arranged in order of increasing water depth.


Sample
Dacrydium cupressinum
Dacrycarpus dacrydioides
Podocarpus ferrugineus
Weinmannia racemosa
Quintinia acutifolia
Elaeocarpus
1
2
3
4
5
6
7
8
9
0 10 20 30 35
0 10 20
0 10
0 10 20 25
0 10 20
0 5
increasing depth
Sample
Coprosma
Metrosideros
Myrsine
Griselinia
Cyathea smithii
Dicksonia squarrosa
0 5
0 10 15
0 5
0 5
0 10 20
0 5
increasing depth
% Total Basal Area for tree species in vegetation
% pollen (Pollen Sum = total pollen and spores)

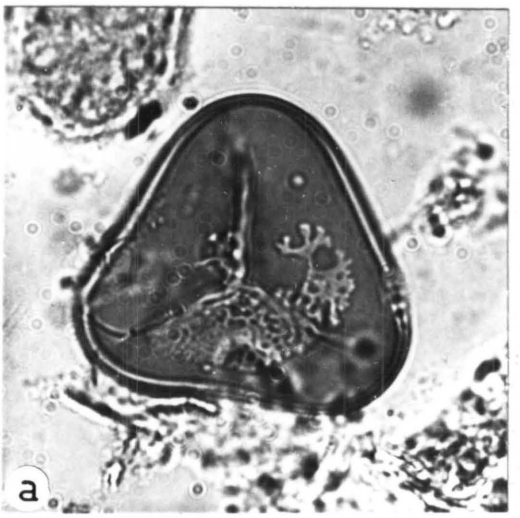
An inspection of *Cyathea smithii* spores and *Dacrydium cupressinum* pollen from seven samples reveals varying degrees of exine corrosion (Table 8) but in all instances the *Cyathea* spores are more corroded than the pollen of *D. cupressinum* (Figures 55a,b,c illustrate exine corrosion in *Cyathea*). It is generally accepted that fern spores are more resistant to corrosion than pollen (Havinga 1964), therefore the high incidence of corroded *Cyathea* spores in the lake samples possibly results from inwash from soil, and exposed stream banks. Samples 2-5 are near the input area of Sam Creek so inwash may well account for the observed over-representation of *Cyathea* in these sediments. Conversely, the under-representation of *Dacrycarpus* may relate not only to low pollen production but also poor preservation of pollen in moss polsters and surface lake sediments. Lake and pond sediments are reported to be more destructive of exines than *Sphagnum* bog (Sangster and Dale 1964). The low percentages of Cyperaceae pollen in the lake sediments suggest that it is either produced in small quantities; or its proportion in the sediment is reduced by tree pollen, or there is a high corrosion factor.

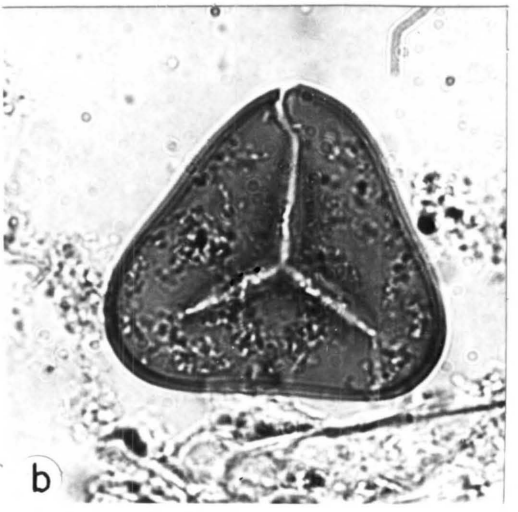
Table 8. Percentage corrosion of the surface of *Cyathea smithii* spores and *Dacrydium cupressinum* pollen. (In all cases 100 pollen/spores were scored).

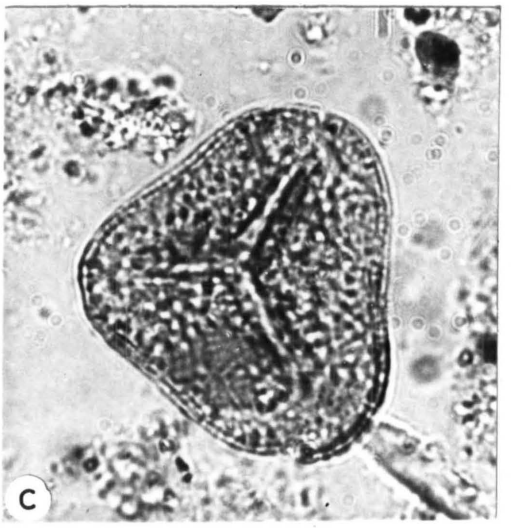
Sample	*C. smithii*			*D. cupressinum*	
	Uncorroded (< 5%)	> 5% corrosion	>30% corrosion	Uncorroded (< 5%)	Corroded (> 5%)
PHa	89	11	-	-	-
PHc	-	-	-	92	8
DDd	-	-	-	98	2
2	58	21	21	67	33
3	62	22	16	74	26
4	54	25	21	72	28
5	45	31	24	77	23

Figure 55. Exine corrosion in *Cyathea smithii* spores (x 1000).

a. more than 5% (bacterial?)
b. less than 5%
c. more than 30%.


a


b


c

Pollen percentages of most taxa in the lake sediment samples are relatively constant over the whole lake basin. Such constancy compares favourably with forest samples which frequently reveal local dominance of the species (e.g. DDd - *Dacrydium cupressinum*) and so provides a basis for supporting the use of lake sediments for palaeoecological investigation. MacPhail (1975) concluded that pollen assemblages in lacustrine samples in Tasmania reflect more accurately both the local and extra-local plant association in the environs of the sample site than do moss polster or trap samples. Davis (1968) postulates that repeated redeposition of pollen from the sediment surface during periods of water circulation reduces variation in the percentages of different pollen types in the sediment.

Redeposition probably occurs at Lady Lake as the water is stratified from December to March each year and is then followed by a period of recirculation of the entire volume of the lake (Dr V.M. Stout, pers. comm.). Thus it can be envisaged the mixing of pollen within the water to be followed by redeposition over the whole lake floor resulting in uniform pollen accumulation under all water depths. There are departures from uniformity. *Dacrydium cupressinum* shows no consistent pattern of deposition throughout the entire lake basin, while *Quintinia* and *Podocarpus ferrugineus* show variation with water depth; *Quintinia* appears to increase in proportion to water depth while *P. ferrugineus* is more frequent in near shore sediments. *Quintinia* pollen may provide some evidence for the sorting of pollen types according to their different settling rates, as suggested by Davis and Brubaker (1973) for *Quercus* and

Ambrosia pollen. Enrichment of near shore sediments with *P. ferrugineus* pollen is probably due to differential flotation. Hopkins (1950) found that enrichment of *Pinus* pollen values near lake shores in the United States of America was undoubtedly caused by their tendency to float (Davis and Brubaker 1973) and to be transported by wind and wave action to inshore areas. *P. ferrugineus* pollen is similar in size and morphology to *Pinus* pollen and it shows similar behaviour with the near shore samples (1 to 5 inclusive) containing higher frequencies than off shore samples (6 to 9 inclusive). Mildenhall (1978) observed a similar phenomenon with *Podocarpus* spp. in Caswell, Nancy and Milford Sounds, Fiordland. The depositional pattern for *Dacrydium cupressinum* is difficult to interpret although Sample 1, near the western shore of the lake, probably received its pollen from source trees which shed directly on to the water surface. This also has the effect of concealing *Cyathea* spores. Samples 2 to 5 (inclusive) are also near the shore-line but receive their *D. cupressinum* pollen from the trunk space (refer Tauber 1967), as atmospheric fallout, and possibly inwash, but the deep water samples (6 to 9 inclusive) show greater variance for *D. cupressinum* pollen probably as a result of redeposition and fallout.

The last three examples indicate that significant differences in the proportions of pollen types can occur in surface sediment at different water depths in the same lake. This raises the difficult question (as Davis, Brewster and Sutherland (1969) did) about the validity of using a single core of lake sediment for the study of past

vegetation and climates. Not only do the characteristics of the vegetation need to be taken into account but also the behavioural characteristics of pollen in transit to the lake sediment. It is possible that if enough cores from different sites in a region are available for study then a trend may develop which could help in interpretation of data from any one site.

7.7 POLLEN TO MACROFOSSIL REPRESENTATION

A recent study of modern macro-plant remains (potential macrofossils) in Lady Lake (Drake 1977) permits comparison with the basal area and pollen data. The results of both studies are broadly similar but where there is poor representation in one kind of data some counterbalance can be sought from the other. For example, *Podocarpus ferrugineus* is over-represented in the lake litter but more closely represented by pollen to the vegetation while *Quintinia* and *Cyathea smithii* show the opposite trend. *Dacrycarpus dacrydioides* and Cyperaceae are under-represented by pollen and potential macrofossils. The under-representation of Cyperaceae is considered notable (Drake 1977) since these plants are ideally placed to contribute fossils to the lake sediment. The pollen data did not indicate the existence of either orchids or *Nertera* spp. (normally under-represented in modern pollen spectra and probably subject to rapid decay), whereas the lake litter did. One advantage lake litter sampling has over pollen analysis is that it provides the opportunity to identify specimens to the species level when generally pollen analysis tends to indicate only at the family and generic level. The usefulness of macrofossils to support

pollen analytic data is clearly evident; they enlarge the list of identifiable species, provide evidence of local presence, and define the earliest certain time of local arrival for migrating species (Watts 1978), but their relative presence is very much dependent on suitable conditions for their preservation (Lintott and Burrows 1973) and gaps may simply record unsuitable conditions. In this respect pollen is less sensitive.

Despite the various shortcomings of both methods they are complementary and whenever possible should be used together to give a more accurate and complete indication of the nearby vegetation. Particular areas of application in New Zealand pollen analysis are the *Dacrydium bidwillii - biforme* complex which has been discussed in Chapter 4 and the *Nothofagus fusca* group which frustrates much of the interpretation of pollen diagrams.

7.8 SUMMARY OF POLLEN AND SPORE REPRESENTATIVITIES

Table 9 summarises the results for pollen and spore types recorded in this study (i.e. Chapters 5, 6 and 7). Estimates of their representations and relative export are provided in addition to information on their pollination mechanism. The species are listed as they appear on the pollen diagrams and in Appendices I and II.

The terms over-, well- and under-represented have been defined in Chapter 5. Relative dispersal powers of pollen and spores are classified according to Flenley (1973) in terms of high, medium or low relative export. Taxa represented in the vegetation surveys at the point of sampling but not recorded in the pollen spectra are

considered to have low relative export; while those consistently recorded in the pollen rain when not present in the immediate vegetation show high relative export. It must be stressed that a species may be over-represented, but have low relative export, while others may be under-represented but show medium to high relative export in the form of long-distance transport. In most cases the on-site vegetation is very important in governing pollen representation. Taxa with a low relative export recorded in frequencies of >10%, probably reflects on-site or near-site deposition.

*A = Anemophilous

E = Entomophilous

O = other forms of pollination (e.g. birds, water)

Table 9. Representation and dispersal power of pollen and spore types in New Zealand. A summary based on surface spectra results presented in Chapters 5, 6 and 7. See text for details.

NO.	NAME ON DIAGRAMS	POLLINATION MECHANISM*	REPRESENTATION			DISPERSAL POWER (RELATIVE EXPORT)			NOT SUFFICIENT DATA	COMMENTS
			OVER-	WELL-	UNDER-	HIGH	MED.	LOW		
1	*Dacrycarpus dacrydioides*	A			+		+			>10% signifies on-site deposition. Normally under-represented in a forest sample but often recorded upslope in higher altitude samples where local vegetation consists of low pollen producing species.
2	*Dacrydium cupressinum*	A	+			+	+			High pollen production leads to good local representation. Often poorly recorded in dense forested stands due to high trunk space component from local vegetation.
3	*D. colensoi*	A			+			+		Always in low numbers.
4	*Libocedrus*	A		+	+			+		Extremely variable and percentages depend to large extent on pollen production of surrounding vegetation. Anomalous recording at Meins Knob largely unexplained.
5	*Podocarpus ferrugineus*	A		+	+		+			Large, probably bouyant grain permits good export. Frequently masked by *D. cupressinum* with which it is commonly associated.
6	*Podocarpus spicatus*	A			+		+	+		Recorded in low numbers except at Ajax Hill where high frequencies due to uplift from lower altitudes.
7	*P. totara*	A							+	
8	*P. totara* var. *waihoensis*	A		+			+			Recorded only at Evans Road, Harihari where good export into low forest.
9	*P. hallii*	A		+				+		Well recorded near (<20 m) source plants.
10	*Nothofagus fusca* type	A	+	+		+				Dispersed vast distances and discontinuities in representation probably brought about by variability in sample age.
11	*N. menziesii*	A			+		+	+		Often compared with *N. fusca* type with mostly unfavourable results. Sometimes widely dispersed e.g. recorded on Stewart Island having origin in Southland forests.
12	*Pinus*	A				+				Exotic which is well dispersed.
13	Myrtaceae	A,E,O			+			+		Infrequent in spectra.
14	*Carpodetus*	E			+			+		Seldom recorded although present at many sites. Pollen grain a large tetrad.
15	*Quintinia*	A,E		+			+			Consistently present in most surface samples.
16	*Elaeocarpus*	E			+			+		Small pollen grain and mostly under-represented, although at Evans Road gives a high frequency probably from past elements in the vegetation.
17	*Aristotelia*	E			+			+		Recorded in low but consistent numbers.
18	*Pseudopanax*	E	+	+				+		Over-represented at MOAST-4 otherwise well recorded but only when near the site.
19	*Pittosporum*	E			+			+		Seldom recorded in pollen spectra; appears to have delicate pollen.
20	*Fuchsia*	E,O			+			+		Distinctive pollination mechanism permits little aerial transfer of pollen. When recorded a definite note of local presence.

Table 9 (Cont'd)

NO.	NAME ON DIAGRAMS	POLLINATION MECHANISM*	REPRESENTATION			DISPERSAL POWER (RELATIVE EXPORT)			NOT SUFFICIENT DATA	COMMENTS
			OVER-	WELL-	UNDER-	HIGH	MED.	LOW		
21	*Pseudowintera*	E			+			+		Large pollen grain which is produced in low numbers leads to dramatic under-representation.
22	*Schefflera*	E			+			+		Under-represented at Harihari and Saltwater II.
23	*Pennantia*	A,E		+	+			+		A non-specialised insect modified flower results in an open flower which occasionally sheds abundant pollen, especially at Saltwater II.
24	*Hoheria*	A,E							+	Not recorded in vegetation sampled.
25	*Plagianthus*	A,E							+	As above.
26	*Melicope*	E			+			+		Recorded at AH-CB, Ajax Hill.
27, 28	*Metrosideros*	A,E,O		+	+			+		Often well recorded and probably due to abundance of lianes. Pollen falls close to source plant.
29	*Weinmannia*	E			+			+		Important forest species but always poorly recorded. Little uplift at desirable sites (Ajax Hill, Stewart Island) thus low relative export. High frequencies with the exclusion of most others would signify a dense stand.
30	*Griselinia*	E		+	+			+		Recorded in low numbers except at MOAST-4 where it is well represented.
31	*Laurelia*	E			+			+		Infrequent at Harihari where it is present.
32	*Pomaderris*	A,E							+	
33	*Ascarina*	A		+			+			Consistently recorded, especially near source plants.
34	Compositae	E	+	+	+			+		Representation difficult to ascertain due to complexity of sources in the type. *Raoulia* appears to be over-represented with extremely low relative export, while shrub Compositae seem to be extremely poorly represented.
35	*Plantago*	A,E			+			+		Under-represented at OMAN S1 where recorded in the vegetation.
36	*Coprosma*	A,E	+	+			+			Complexity of sources and anemophily results in its consistent presence.
37	*Coriaria*	E							+	Trace frequencies recorded at Flax Road and Snake Creek.
38	*Dracophyllum*	E		+	+			+		Despite abundance at many sites barely recorded. Well recorded at AH-SW3 only.
39	*Myrsine*	E			+			+		Under-represented which probably reflects dominance of other species in the vegetation. In shrubland may be better represented.
40	Scrophulariace	E			+			+		Seldom recorded when present at many sites.
41	*Pentachondra*	E			+			+		As above.
42	*Phyllocladus*	A	+	+		+	+			Subject to long-distance transportation; often variable representation at many sites due to vegetation structure and association with other taxa.
43	*Dacrydium intermedium*	A		+			+			Quite well recorded at Stewart Island where frequent on wet or exposed sites.

Table 9 (Cont'd)

NO.	NAME ON DIAGRAMS	POLLINATION MECHANISM*	REPRESENTATION			DISPERSAL POWER (RELATIVE EXPORT)			NOT SUFFICIENT DATA	COMMENTS
			OVER-	WELL-	UNDER-	HIGH	MED.	LOW		
44, 45	*Dacrydium biforme-bidwillii*	A		+	+		+			Extremely variable in presence (especially *D. biforme*).
46	*Casuarina*	A	+			+				Long-distance transportation, mostly from Australia.
47	*Leptospermum*	A,E		+	+			+		At Evans Road, where abundant in the vegetation, well recorded but at Stewart Island where widespread at higher altitudes under-represented. Therefore variable with poor export capabilities.
48	*Salix*	A				+				Exotic and well dispersed.
49	*Cyathodes*	E			+			+		Recorded when close to a source plant.
50	Chenopodiaceae	A				+			+	Well dispersed as not present in vegetation at all sampling sites.
51	*Muehlenbeckia*	A	+					+		Ineffective dispersal and over-represented at sites MOAST-5 and NTHST.
52	*Rubus*	E			+			+		Seldom recorded in surface samples.
53	*Ripogonum*	A	+					+		At Harihari slightly over-represented. Not recorded in other samples.
54	*Colobanthus*	E							+	
55	*Epilobium*							+		Refer comments for *Fuchsia*. Recorded MOAST-5
56	*Drapetes*	E			+			+		Infrequent but when recorded important indication of local presence.
57	cf. *Discaria*	A,E		+				+		Near site only, e.g. WILBFN.
58	Gramineae	A	+			+				Well recorded but low proportion transported into forested areas.
59	*Astelia*	A		+				+		Mostly infrequent, short distances away from source.
60	*Collospermum*	E			+			+		Long-distance transport was observed at Lady Lake but generally poorly recorded.
61	*Acaena* (Rosaceae)	E			+			+		Not frequently observed.
62, 63	Umbelliferae	E		+	+			+		Often frequent near source.
64	Cruciferae	E			+			+		Infrequent except at KIWIFT and AH-CB.
65	*Taraxacum*	E	+	+				+		Over-represented at OMAN S2 when present near site.
66	*Rumex*	A			+			+		Recorded in low numbers.
67	*Ranunculus*	E			+			+		As above.
68	*Earina*	E			+			+		Only recorded at Harihari where abundant at site of deposition.
69	*Calorophus* (*Empodisma*)	A			+			+		Under-represented at AH-CB; low pollen production (?).
70	Restionaceae	A							+	
71	*Typha*	A							+	
72	*Myriophyllum*	A		+				+		Recorded at MKB-T near source plants.
73, 74	*Gunnera*, *Haloragis*	A							+	

Table 9 (Cont'd)

NO.	NAME ON DIAGRAMS	POLLINATION MECHANISM*	REPRESENTATION			DISPERSAL POWER (RELATIVE EXPORT)			NOT SUFFICIENT DATA	COMMENTS
			OVER-	WELL-	UNDER-	HIGH	MED.	LOW		
75	*Phormium*	O			+			+		Infrequent in Lady Lake samples when predominant on lake edge.
76	Cyperaceae	A		+	+			+		Surprisingly restricted in its distribution away from site. Well represented at MKB-T.
77	*Cyathea smithii*	A	+					+		Poor export of spores but often over-represented due to proximity to source. High spore producer.
78, 79	*C. dealbata*, *C. medullaris*	A							+	
80	*Dicksonia fibrosa*	A							+	
81	*D. squarrosa*	A		+				+		Well represented inside forest, but large spore results in limited dispersal.
82	*D. lanata*	A							+	
83	*Pteridium*	A			+			+		Under recorded at Lady Lake.
84, 85, 86, 87	*Lycopodium* (includes *L. fastigiatum*, *L. scariosum*, *L. laterale*, *L. ramulosum*)	A		+				+		Often abundant in vicinity of source.
88	*Phymatosorus*	A	+					+		Not seen outside vegetation containing its source plants.
89	*Polystichum*	A		+				+		Recorded at FANGST.
90	*Pyrrosia*	A							+	
91	*Blechnum*	A		+			+			Recorded consistently.
92	*Asplenium*	A		+			+			As above.
93	*Gleichenia*	A			+			+		Poor record at Lady Lake.
94	*Hymenophyllum*	A			+			+		Low numbers recorded although frequent.
95	Monolete spores	A		+					+	Represents a complex source including 91 and 92.
96	*Histiopteris*	A							+	Not often present at site.
97	*Hypolepis*	A							+	As above.

CHAPTER 8

ARANUIAN VEGETATION FROM LADY LAKE, NORTH WESTLAND

8.1 INTRODUCTION

The Aranuian (post-glacial) is thought by Suggate (1965) and Suggate and Moar (1970) to have begun with the retreat of the Otiran glaciers at about 14,000 years ago while Lintott and Burrows (1973) consider it should coincide with the transition from a *Dacrydium - Coprosma* environment to a *Phyllocladus* environment (observed at Cass, South Island) at about 10,000 years B.P. Subsequent patterns of vegetation were influenced by a climatic sequence of warming and cooling (Cranwell and von Post 1936). Molloy (1969) and Moar (1971) have emphasised, from the slow rate of spread of *Nothofagus*, that the vegetation is still recovering from the disruptive effect of the Otira glaciation and thus major changes as illustrated by pollen diagrams do not necessarily reflect major changes in climate.

Since Lady Lake is situated in north Westland this discussion will concentrate on vegetation changes recorded for the Westland region of the South Island. The sites mentioned in the text are shown in Figure 56.

In a radiocarbon dated profile from Crooked Mary Creek, Springs Junction, north Westland (Moar 1971), a *Phyllocladus/Dacrydium bidwillii-biforme* shrubland was replaced about 8,000 years ago by *Podocarpus - Dacrydium cupressinum* forest which in turn was rapidly overshadowed by *Nothofagus* (pollen

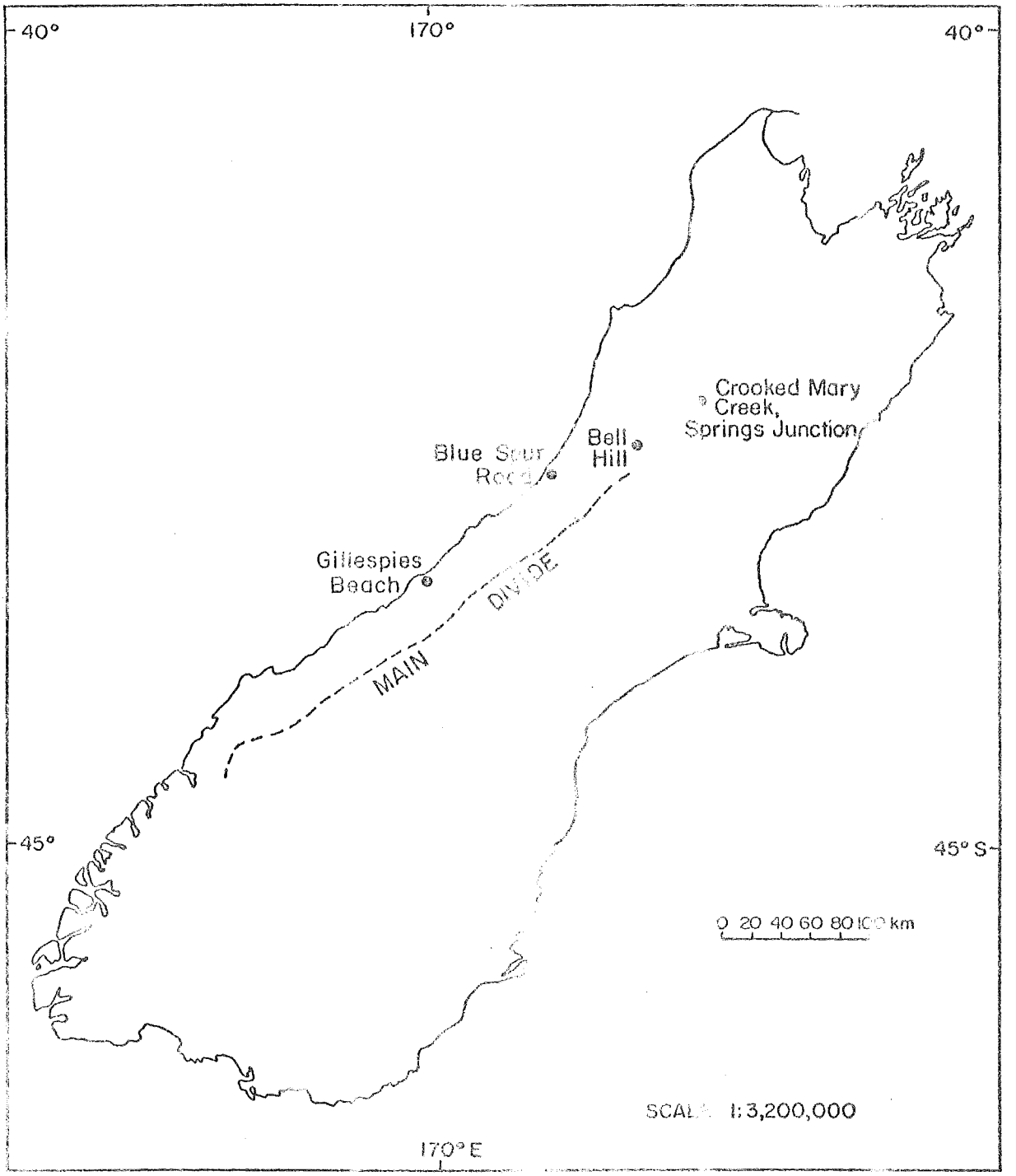


Figure 56. Aranuian sites in Westland.

of the *N. fusca* type). At Bell Hill, approximately 50 km south-west of Crooked Mary Creek the trend is from grassland to *Coprosma-Myrsine* shrubland to *Weinmannia* forest at about 10,000 years B.P. followed by complete domination of *Dacrydium cupressinum* forest until 2,400 years when *Nothofagus* is thought to have begun to advance from the north (Moar 1971). Fifty kilometres south of Bell Hill at Blue Spur Road, Hokitika, a similar *Dacrydium cupressinum* forest existed (Moar and Suggate 1973), but this is undated. A similar vegetation sequence is recorded at Gillespies Beach Road some 160 km south of Bell Hill (Moar 1973) with *Coprosma-Myrsine* shrubland present around 11,000 years ago.

A general pattern is beginning to emerge from Westland but each site shows local variation which emphasises the diversity and complexity in the development of Aranuian vegetation. The aim of the present work is to provide more information and assist in differentiating Aranuian vegetation patterns.

8.2 STUDY METHODS

A site description has been provided in Chapter 7. A 7 m deep section of peat, close to the road at the eastern extreme of the lake (Figure 57) was sampled. Samples for radiocarbon assay were taken at 2.95 - 3.05 m, 6.70 - 6.80 m and 6.95 - 7.05 m. In addition to the pollen analysis of the peat sequence macrofossils were identified at 6.70 - 6.80 m and 6.95 - 7.05 m.

Moar (1971) recorded pollen spectra from this site at 5.35 m, 5.55 m and 5.60 m. Results obtained from the modern

Figure 57. Aerial view of Lady Lake. The core site is marked by a white cross (Crown Copyright).

pollen spectra (presented in Chapter 7) analysed from Lady Lake are used to aid interpretation of the Lady Lake pollen diagram which is then discussed in the context of earlier work.

8.3 RESULTS AND DISCUSSION

The pollen diagram and macrofossils identified from Lady Lake are presented in Figure 58 and Table 10 respectively. The diagram has been zoned on the basis of percentage changes of the predominant pollen types. These zones are designed to assist in the discussion of the diagram and their boundaries, in years B.P., have been estimated on peat accumulation rates. The radiocarbon dates indicate that organic deposition at the core site began about 5,700 years B.P.

Stratigraphy noted at the point of sampling was as follows:

0 - 1.50 m	watery sedge peat with many gaps
1.50 - 3.50 m	fibrous sedge peat becoming more compacted with depth; wood scattered throughout - possibly *Dacrycarpus*
3.50 - 5.45 m	sedge peat
5.45 - 5.55 m	water layer not sampled
5.55 - 6.80 m	fibrous sedge peat with wood at 6.73 m
6.80 - 7.25 m	grey gritty clay becoming more compacted with depth and containing some organic matter

Table 10. Macrofossil remains identified from peat at Lady Lake, North Westland

Taxa	6.70 - 6.80 m			6.95 - 7.05 m		
	Fossil Type			Fossil Type		
	Seed	Leaf	Other	Seed	Leaf	Other
Dacrycarpus dacrydioides	+	+			+	Male cone
Podocarpus ferrugineus	+	+		+	+	Root nodules
P. spicatus			Bark			Root nodules
Dacrydium cupressinum	+	+		+	+	
Weinmannia racemosa				+		
Pseudowintera colorata					+	
Coprosma propinqua		+				
Coprosma spp.	+			+		
Monocotyledon					+	
Pteridophyte						Stem
Musci				+	+	

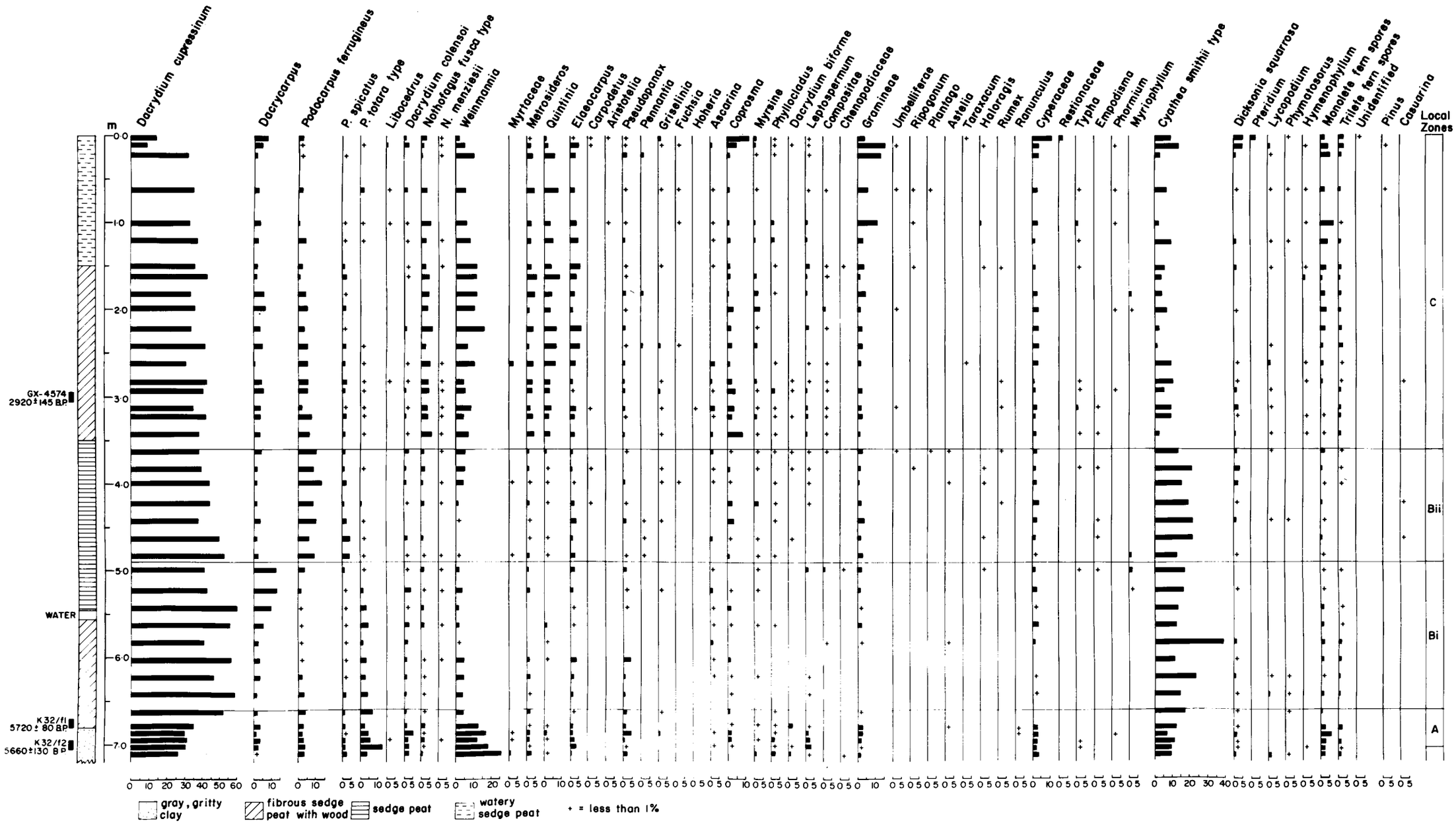
Zone A: 7.05 - 6.60 m 5700 - 5400 year B.P.

The base of the diagram is characterised by high pollen frequencies of *Weinmannia*, *Dacrydium cupressinum* and *Podocarpus totara*. Components of a wetland vegetation are present in low percentages *viz.* *Dacrydium colensoi*, *Leptospermum*, *Dacrycarpus* and Cyperaceae. This implies their local presence at the time since *D. colensoi* and *Dacrycarpus* are typically under-represented in modern pollen spectra (refer Chapter 5) and Cyperaceae pollen is not well represented in modern spectra from Lady Lake. At the top of the zone *D. cupressinum* dominates with *Cyathea*, and *Weinmannia* declines to low levels (<5%). *Pseudopanax*, *Podocarpus ferrugineus* and *P. totara* occur at consistently low levels, but in the case of the latter it is uncertain whether this signifies local stands or isolated individuals as little is known of its pollen representation. The main species are well represented by macrofossils

Figure 58. Pollen diagram for Lady Lake.

POLLEN DIAGRAM, LADY LAKE, WESTLAND

POLLEN SUM : TOTAL POLLEN AND SPORES


m
0·0
1·0
2·0
3·0
4·0
5·0
6·0
7·0
GX-4574
2920±145 B.P.
WATER
K32/11
5720±80 B.P.
K32/12
5660±130 B.P.
Dacrydium cupressinum
Dacrycarpus
Podocarpus ferrugineus
P. spicatus
P. totara type
Libocedrus
Dacrydium colensoi
Nothofagus fusca type
N. menziesii
Weinmannia
Myrtaceae
Metrosideros
Quintinia
Elaeocarpus
Carpodetus
Aristotelia
Pseudopanax
Pennantia
Griselinia
Fuchsia
Hoheria
Ascarina
Coprosma
Myrsine
Phyllocladus
Dacrydium biforme
Leptospermum
Compositae
Chenopodiaceae
Gramineae
Umbelliferae
Ripogonum
Plantago
Astelia
Taraxacum
Haloragis
Rumex
Ranunculus
Cyperaceae
Restionaceae
Typha
Empodisma
Phormium
Myriophyllum
Cyathea smithii type
Dicksonia squarrosa
Pteridium
Lycopodium
Phymatosorus
Hymenophyllum
Monolete fern spores
Trilete fern spores
Unidentified
Pinus
Casuarina
Local Zones
C
Bii
Bi
A
0 10 20 30 40 50 60
0 10
0 10
0 5 0 10 0 5 0 5 0 5 0 5 0 5 0
0 10 20
0 5 0 5 0 10 0 5 0 5 0 5 0 5 0 5

(Table 10) with the exception of *P. totara* and *Weinmannia*. By about 5700 radiocarbon years ago *D. cupressinum* forest was well established (K32/f1: 5720 ± 80 years B.P. and K32/f2: 5660 ± 130 years B.P.).* Consequently this diagram does not record the spread of *D. cupressinum* forest dated at 9000 years ago at Bell Hill, north Westland (Moar 1971). Moar's date cannot be corrected for secular effect and is consequently not relative to the new dates reported in this chapter.

The high percentage of *Weinmannia* pollen at the base may be a consequence of falling lake levels resulting in the exposure of new soil and wet ground. Wardle (1965) reported good seedling growth of *Weinmannia* in Westland under these conditions. Eventually, *D. cupressinum* seedlings probably entered the vegetation and finally suppressed the *Weinmannia* canopy. Evidence for this is a fall in *Weinmannia* and a dramatic rise in *D. cupressinum* pollen to 60% of the pollen sum within a short time. Although over-shadowed *Weinmannia* remained an important element in the vegetation.

Zone Bi: 6.60 - 4.90 m 5401 - 4400 yr B.P.

This zone is dominated by *Dacrydium cupressinum* and *Cyathea*. *D. cupressinum* represents the maximum expression of the post-glacial development of podocarps in Westland and has been

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*The radiocarbon date obtained for 6.70 - 6.80 m (K32/f1) is older than the date obtained for 6.95 - 7.05 m (K32/f2). The reason for this is not known but due to an overlap at the maximum possible expression of the errors it was not considered erroneous. The initial organic depositional rate therefore appears to be rapid.

observed in many diagrams which is usually attributed to the warm moist conditions of the climatic optimum (Molloy 1969). However, as Molloy stresses, the podocarp forests are difficult to interpret climatically because of the number of species involved and their ecological amplitudes are little known. Wide ecological amplitudes of *Dacrycarpus dacrydioides* (Wardle 1974) make it difficult to interpret the rise in *Dacrycarpus* pollen near the top of the zone (5.40 m). It is unclear whether either a rise in lake level inducing moist ground conditions, or a fall in lake level exposing moist ground conditions is responsible for the increase of *Dacrycarpus* pollen reflected in the pollen peak of 14%. As *Myriophyllum* pollen appears in this zone it lends weight to a hypothesis that lake levels fluctuate to cover or expose the core site. Values of *Dacrycarpus* as high as 10-12% signify on-site deposition, thus the *Dacrycarpus* rise can be considered to reflect a local change in the vegetation and not one of regional extent. *Dacrycarpus* swamp forest persists at the northern, eastern and southern margins of Lady Lake today (refer Figure 47). *Podocarpus totara* maintains a level of 3.5% until near the top of the zone.

Zone Bii: 4.90 - 3.60 m 4400 - 3500 yr B.P.

Dacrydium cupressinum and *Cyathea* remain at high levels for most of the zone then decline toward the top. Other significant features here are a rise in *Podocarpus ferrugineus*, *P. spicatus* and *Weinmannia* pollen values at 4000 years ago (date estimated on a peat accumulation rate of 1.2 mm yr^{-1}). *Dacrycarpus* remains close to the core site and is important in the local vegetation. Due entirely to the high levels

for *D. cupressinum*, which continue from the previous zones, other species are almost completely excluded until near the top when the hardwoods *Elaeocarpus*, *Metrosideros*, *Coprosma* and *Ascarina* become prominent. These represent a mixed podocarp/ hardwood association which persists to the present day.

Zone C: 3.60 m - 0.00 m 3500 years B.P. - Present Day

Dacrydium cupressinum continues to decline and matches changes shown in Westland diagrams from elsewhere (Moar 1971, 1973). Nevertheless, *D. cupressinum* remains the most common pollen type. In general the spectra here resemble the modern pollen rain recorded from lake sediments discussed in Chapter 7. At the base of the zone there is a small consistent rise in percentages of *Nothofagus fusca* type pollen. This has also been observed by Moar (1971) at Nan's Kettle and is estimated to occur at about 3500 B.P. A similar age is determined for this diagram from a radiocarbon date (GX 4564; 2920 ± 145 years B.P.) for the 3.00 m level. The age has been corrected for secular effect by the method of Damon, Long and Wallick (1972). This leads to the same conclusion reached by Moar (1971) that the slight rise represents the approach of *Nothofagus* from the north. An increase in *Quintinia*, *Elaeocarpus*, *Metrosideros* and *Weinmannia* pollen suggest their increasing importance in a vegetation in which the canopy has opened due to a decline in the dominance of *D. cupressinum*.

Large fluctuations of about 10% in the percentages of *Cyathea* spores intimate that this type had a patchy distribution near the core site. Previous work (Chapters 5 and 7) has shown that *Cyathea* has abundant spore production but relatively poor dispersal. *Ascarina* maintains low but

consistent levels from about 5000 to 3000 years B.P. but then almost disappears. This trend has been discussed by McGlone and Moar (1977) who postulate it to be due to the increased incidence of frost and drought.

Swamp vegetation remained close to the site of deposition as evidenced from the constant records of *Dacrydium colensoi* and Cyperaceae pollen. Rising percentages of Gramineae at about 0.40 m might coincide with the arrival of Polynesians whom Holloway (1954b) suggests were in Westland about 1000 years ago. The only dates available in Westland are from charcoal collected in the Buller River mouth in archaeological sites (Moore and Tiller 1975). These give dates of 619 and 710 years B.P. Most records of the influence of the Polynesians and their burning practices come from sites on the east of the Main Divide (Cranwell and von Post 1936; Harris 1963; Moar 1970, 1971) and although burning may not have been of such magnitude in Westland it would have had some role in forest destruction. This so called "revertance" of grass pollen (Molloy 1969) reaches a peak at 0.20 m with forest clearance by Europeans. This is substantiated by falling percentages of hardwood pollen and the appearance of introduced *Pinus* pollen in the uppermost levels.

8.4 CONCLUSION

The pollen diagram from Lady Lake described and discussed above reaffirms the diversity of post-glacial forest types already noted by Moar (1971, 1973). There were localised changes in the vegetation resulting from probable changes in the character of the lake. Such local

fluctuations, although not indicating any major climatic or vegetational trends, are important when reconstructing Aranuian vegetation from pollen diagrams. The interpretation has been assisted by a study of the modern pollen spectra at Lady Lake (Chapter 7 results) but a detailed interpretation is frustrated by a paucity of information on the ecology of some of the more important forest species, such as *Dacrycarpus* and *Podocarpus ferrugineus*, and difficulties in interpreting lake sediment pollen spectra.

CHAPTER 9

CONCLUSIONS

The substantive findings of this work have been presented and discussed in the previous chapters. The purpose of this chapter is to examine the results in the broader context of the field and to derive from these the implications of the work. The data has raised more questions than it has answered but this is probably inevitable in an area in which little previous work has been done. Suggestions for future research are based on the unanswered questions.

Pollen analysts must first become conversant with the pollen of the wide range of types likely to be encountered in a modern or fossil sample. In New Zealand, however, so little work has been published on the morphology of the pollen of most plants that often it is first necessary to become a pollen morphologist. The New Zealand gymnosperm pollen can be divided into morphologically distinct groups, but within each group some pollens remain difficult to identify. Two groups which pose the most difficult problems are *Dacrydium bidwillii* and *D. biforme*, and the *Podocarpus totara* group. *Dacrydium kirkii* is also very similar to *D. bidwillii* and *D. biforme* but can usually be identified on a size basis. With the exception of *Podocarpus nivalis* and possibly *P. hallii* the ecological ranges of species in the *P. totara* group are similar and the need for specific identification is not as

great as where the ecological ranges are very different. The pollen grains of the three species of *Phyllocladus* are inseparable. The scanning electron microscope reveals subtle differences in the morphology of the proximal cap but this is of little value for routine pollen analysis carried out with the light microscope. Speculation about the identity of *Phyllocladus* pollens can be made usually from a knowledge of the present day distributions and ranges of the three species as well as those of the plants associated with them in a fossil sample. Obviously, if *Phyllocladus* pollen is associated with pollen from plants which are strictly alpine it will not be that of *P. trichomanoides* and may not even be *P. glaucus*. This can similarly be applied to the pollen of *Libocedrus* as *L. bidwillii* has a substantially different range and ecology to *L. plumosa*.

Two morphological features not previously described in New Zealand gymnosperm pollen are the region of 'weakness' found in *Podocarpus spicatus*, *P. ferrugineus*, *Dacrydium colensoi*, *Dacrydium intermedium* and all species of *Phyllocladus*; and the pseudopore region found in *Libocedrus*. It is thought that the zone of 'weakness' may function in harmomegathic responses but this needs further investigation. The pseudopore region in *Libocedrus* has been shown, through wetting experiments, to have no function in germination (Chapter 4).

Modern pollen rain studies in lowland and montane forests, grassland and on cushion bogs have been employed to establish guidelines for the dispersal and thus representation of major plants in these vegetation types. Representation is shown not to be in the order of source species proportion in the vegetation and the summary of

pollen representations (Table 9) based on the record of pollen in all surface samples provides confirmation of this. Comparison of pollen percentages in modern spectra with a quantitative survey of the vegetation has allowed a more accurate assessment of representations. Although this is successful it is considered that comparisons are best made on a larger scale and complete forest inventories of the type available to North American and Canadian pollen analysts could be used.

There are limitations in the use of moss cushions and lake sediments as indicators of modern pollen rain because various forces act on the sample prior to collection, during its preparation and in the final analysis. These are often manifest in under-representation of plants and include the modes of pollination and thus pollen production, the differential preservation of the pollen, the size of the plant which often restricts dispersal, misidentification during the counting process and long-distance transport. Because there is under-representation of some pollen types some plant groups (all wind-pollinated) are over-represented and consequently the pollen rain presents a false picture of the original vegetation.

Due to the size of New Zealand, the complexity of vegetation types and the wide dispersal of some pollen types it is not possible to identify 'type spectra'. Local vegetation is often easily recognised in surface samples analysed from within forested areas while regional vegetation is best recorded in open bog sites (e.g. Ajax Hill, South-east Otago and Stewart Island) because the local species are low pollen producers. Marked regional differences in

vegetation make it possible to detect instances of pollen and spore dispersal from one region to another by way of long-distance transport. There is little doubt that pollen once lifted into the upper atmosphere will travel vast distances. Several island studies and the presence of *Dacrydium cupressinum* pollen in surface samples in Canterbury provide evidence for this.

Pollen dispersal is a problem of particular importance and can only really be appraised through a series of long-term trapping programmes. A recent article by Moar and Myers (1978) reports on the implementation of such a programme and the potentialities of the method are clear. In this thesis traps were used but the design was not suitable for the high precipitation encountered in Westland. Flenley (1973) used a modified Oldfield trap to study the pollen rain from tropical vegetation. This trap collected the pollen in de-oiled acetate yarn by gravity feed which was kept permanently moist by a water reservoir underneath. It was impracticable to fit a reservoir large enough for a year's rainfall so the excess water was drained out of air holes. It is suggested that such a trap would be ideally suited to Westland conditions.

The complementary use of macro plant remains and modern pollen allows a more accurate prediction to be made of the proportion of original vegetation likely to be represented as fossils. Certainly, the pollen and plant remains when used together at Lady Lake, Westland, reflect the modern vegetation to a greater degree than when both are used separately. Studies in this direction, in New Zealand, are limited and the effects of sedimentation and compaction

on macro plant remains are largely unknown. It is likely that pollen is better preserved because of the presence of sporopollenin.

Finally, the results of the pollen morphological and modern pollen rain studies are applied to an investigation of vegetation history. In Westland the vegetation for much of the post-glacial period has been dominated by gymnosperms belonging to the Podocarpaceae. The Lady Lake pollen diagram emphasises the complexities in this vegetation and further sites must be found to allow us to piece together the framework of development. The vegetation of the last 6000 years at Lady Lake is thought to resemble that which is mirrored in modern pollen rain results derived from analysis of moss cushions and lake sediments. This situation may not always hold as plant extinctions could have taken place. There are subtle changes in the vegetation and these are as equally important as the major changes but their interpretation is restricted by the lack of ecological data on the major plant species. Thus it becomes readily apparent that pollen analysts must work in close liaison with botanists, especially ecologists.

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APPENDIX I

The table lists the pollen types and their nearest identification in the Department of Geography, University of Canterbury reference collection. The abbreviation for each type is that which has been used as a heading in the computer listing of raw pollen counts appearing in Appendix II.

NO.	ABBREV.	NAME ON DIAGRAMS	GEOG. DEPT REF. NO.
1	DACP	*Dacrycarpus dacrydioides*	385-2-3
2	D.CU	*Dacrydium cupressinum*	385-1-2
3	D.CO	*Dacrydium colensoi*	385-1-1
4	LIBO	*Libocedrus*	384-1-
5	P.FE	*Podocarpus ferrugineus*	385-2-5
6	P.SP	*Podocarpus spicatus*	385-2-2
7	P.TO	*Podocarpus totara*	385-2-7
8	P.WA	*Podocarpus totara* var. *waihoensis*	285-2-9
9	P.HA	*Podocarpus hallii*	385-2-4
10	N.FU	*Nothofagus fusca*	163-1-2,3,4
11	N.ME	*Nothofagus menziesii*	163-1-1
12	PINE	*Pinus*	-
13	MYRT	Myrtaceae	118-
14	CARP	*Carpodetus serratus*	139-2-1
15	QUIN	*Quintinia acutifolia*	47-1-1
16	ELAE	*Elaeocarpus*	128-1-
17	ARIS	*Aristotelia*	128A-1-
18	PSEP	*Pseudopanax*	212-3
19	PITT	*Pittosporum*	88-1-
20	FUCH	*Fuchsia*	77-1-
21	PSEW	*Pseudowintera*	2-1-
22	SCHF	*Schefflera digitata*	212-4-1
23	PENN	*Pennantia corymbosa*	179-1-1
24	HOHE	*Hoheria*	132-1-
25	PLAG	*Plagianthus*	132-2-
26	MELI	*Melicope*	194-1-
27	METR	*Metrosideros*	118-1-
28	METL	*Metrosideros*	118-1-
29	WEIN	*Weinmannia racemosa*	137-1-1
30	GRIS	*Griselinia littoralis*	209-1-2
31	LAUR	*Laurelia*	11-1-
32	POMA	*Pomaderris*	180-1-
33	ASCA	*Ascarina*	-
34	COMP	Compositae	238-
35	PLAN	*Plantago*	242-1-
36	COPR	*Coprosma*	232-2-
37	CRAR	*Coriaria*	87-1-
38	DRPH	*Dracophyllum*	217-1-
39	MYRS	*Myrsine*	223-1-
40	HEBE	Scrophulariaceae	252-2-

NO.	ABBREV.	NAME ON DIAGRAMS	GEOG. DEPT REF. NO.
41	PENT	*Pentachondra*	-
42	PHYL	*Phyllocladus*	385-3
43	DINL	*Dacrydium intermedium/laxifolium*	385-1-6,7
44	D.BD	*Dacrydium bidwillii*	385-1-3
45	D.BF	*Dacrydium biforme*	385-1-5
46	CASU	*Casuarina*	164-1-
47	LEPT	*Leptospermum*	118-2-
48	SALX	*Salix*	-
49	CYAT	*Cyathodes*	217-3-
50	CHEN	Chenopodiaceae	61-
51	MUEH	*Muehlenbeckia*	57-3-
52	RUBS	*Rubus*	143-3-
53	RIPO	*Ripogonum*	297-
54	COLS	*Colobanthus*	53-1-
55	EPIL	*Epilobium*	-
56	GRAM	Gramineae	332-
57	ASTA	*Astelia*	293-4-
58	COLL	*Collospermum*	293-5-
59	ACAE	*Acaena*	143-2-
60	UMBL	Umbelliferae	213-
61	HYDR	*Hydrocotyle*	213-1-
62	CRUC	Cruciferae	39-
63	TARX	*Taraxacum*	-
64	RUMX	*Rumex*	57-2
65	RANU	*Ranunculus*	15-1
66	EARS	*Earina*	-
67	CALR	*Calorophus (Empodisma)*	330-2-
68	REST	Restionaceae	330-
69			
70	TYPH	*Typha*	-
71	MYRI	*Myriophyllum*	78-1-
72	GUNN	*Gunnera*	78-2-
73	HALO	*Haloragis*	-
74	PHOR	*Phormium*	313-2-
75	CYPR	Cyperaceae	331-
76			
77			
78			
79	C.SM	*Cyathea smithii*	
80	C.DE	*Cyathea dealbata*	413-1-1
81	C.ME	*Cyathea medullaris*	413-1-2
82	D.FI	*Dicksonia fibrosa*	413-2-2
83	D.SQ	*Dicksonia squarrosa*	413-2-1
84	D.LA	*Dicksonia lanata*	-
85	PTER	*Pteridium*	408-2-
86	LYCO	*Lycopodium fastigiatum*	423-1-3
87	L.SC	*Lycopodium scariosum*	-
88	L.LA	*Lycopodium laterale*	423-1-6
89	PHYM	*Phymatosorus*	-
90	POLY	*Polystichum*	414-4-
91	PYRR	*Pyrrosia serpens*	418-1-1
92	GLEI	*Gleichenia*	405-1-
93	BLCH	*Blechnum*	415-1
94	ASPL	*Asplenium*	416-3-
95	HYMN	*Hymenophyllum*	410-1-
96	L.RA	*Lycopodium ramulosum*	-

NO.	ABBREV.	NAME ON DIAGRAMS	GEOG. DEPT REF. NO.
97	MFER	Monolete fern spores	-
98	HIST	*Histiopteris*	-
99			
100	HYPO	*Hypolepis*	-
101			
102			
103	TRIL	Trilete fern spores	-
104	DRAP	*Drapetes*	-
105	DISC	cf. *Discaria toumatou*	18-2-1
106	UNWN	Unidentified	
107			
108			
109			
110			

APPENDIX II. Pollen Counts

This appendix tabulates the pollen counts from all modern samples and the fossil samples from Lady Lake. The modern samples are listed according to site location and the fossil samples according to depth in the core. The abbreviated pollen names are translated in Appendix I. The counts are presented as follows:

(i) Harihari modern samples (in same order as presented in Chapter 5).

(ii) South Island modern samples (in same order as presented on pollen diagram in Chapter 6).

(iii) Lady Lake modern samples (lake samples in order of water depth).

(iv) Lady Lake fossil core. Depths 0-382 cm
Depths 398-705 cm

HARIHARI MODERN SAMPLES

(SALTWATER I, SALTWATER II, FLAX ROAD)

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
SI-A	166	5	0	2	0	0	0	0	0	1	1	0	0	2	5	0	0	2	0	0
SI-B	130	5	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0
SI-C	258	13	3	0	2	0	0	2	0	3	0	0	0	0	5	1	12	5	0	0
SI-D	187	11	2	0	1	0	0	3	0	2	0	0	0	1	1	4	0	2	0	0
SI-E	145	20	10	0	1	0	0	0	0	3	0	0	0	1	6	6	0	13	0	0
SI-F	92	12	1	3	0	0	0	2	0	2	0	0	0	0	14	1	99	1	0	0
SII-A	19	1	0	0	1	2	0	1	0	0	0	0	0	1	5	0	0	2	0	0
SII-B	19	4	1	0	1	6	0	0	0	2	0	0	0	0	5	2	3	0	0	0
SII-C	8	3	0	0	1	4	0	0	0	0	0	0	0	0	15	6	0	5	1	0
SII-D	30	2	5	0	0	3	0	0	0	0	0	1	0	0	8	2	0	0	0	0
FLAX.A	10	150	10	0	5	0	0	0	0	3	0	1	0	0	8	7	6	0	0	0
FLAX.B	6	155	10	0	11	0	0	0	5	2	0	0	0	0	11	1	3	0	0	0
FLAX.C	17	125	5	0	11	0	0	7	6	2	0	0	0	0	7	2	2	1	0	0
FLAX.D	7	201	0	0	10	1	0	1	0	5	0	2	0	0	9	3	1	1	0	0
FLAX.E	13	262	7	0	40	2	0	1	0	6	0	0	0	1	24	9	0	7	0	0
FLAX.F	14	195	19	0	18	0	0	3	1	4	0	4	0	0	16	8	2	1	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COPR	CRAR	DRPH	MYRS	HEBE
SI-A	1	0	0	0	0	0	14	0	16	9	0	0	0	3	0	12	0	0	1	0
SI-B	0	0	0	0	0	0	7	0	36	5	0	0	0	9	0	9	0	0	0	0
SI-C	0	0	0	0	0	0	10	0	3	3	0	0	0	4	4	26	0	0	1	0
SI-D	0	0	0	0	0	0	18	0	6	3	0	0	0	2	0	26	0	0	0	0
SI-E	0	0	2	0	0	0	3	0	49	6	0	0	0	3	0	53	0	0	34	0
SI-F	0	0	1	0	0	0	56	0	40	4	0	0	2	0	0	18	0	0	1	0
SII-A	0	0	33	0	0	0	2	2	6	2	0	0	0	0	0	10	1	0	0	0
SII-B	0	0	10	0	0	0	11	3	8	3	0	0	0	0	0	12	0	0	0	0
SII-C	0	3	33	0	0	0	2	3	21	15	0	0	0	0	1	0	0	0	1	0
SII-D	1	0	91	0	0	0	1	5	5	1	0	0	0	0	0	0	0	0	2	0
FLAX.A	0	0	0	0	0	0	25	0	32	0	0	0	3	0	0	18	3	0	3	0
FLAX.B	0	0	0	0	0	0	6	0	7	0	0	3	0	2	0	14	0	0	8	0
FLAX.C	0	0	0	0	0	0	18	0	56	7	0	0	4	0	0	25	2	0	17	0
FLAX.D	1	0	0	0	0	0	9	0	28	2	0	0	2	0	2	14	0	0	7	0
FLAX.E	0	0	0	0	0	0	15	0	46	3	0	0	4	0	0	25	0	0	3	0
FLAX.F	0	0	0	0	1	0	12	0	24	3	0	0	2	2	0	12	0	0	10	0

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
SI-A	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	27	11	0	0	0
SI-B	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	41	8	2	1	0
SI-C	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	15	12	0	0	0
SI-D	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	22	6	0	0	0
SI-E	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	22	4	0	0	0
SI-F	0	3	0	0	0	0	12	0	0	0	0	0	0	0	0	8	5	0	0	0
SII-A	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4	1	0	0
SII-B	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	12	1	1	0	0
SII-C	0	3	0	0	0	0	0	0	0	0	0	2	3	0	0	8	0	0	0	0
SII-D	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0
FLAX.A	0	17	0	0	0	0	2	0	0	0	0	0	0	0	0	10	3	1	0	0
FLAX.B	0	21	0	0	0	0	0	0	0	0	0	1	0	0	0	23	0	2	0	0
FLAX.C	0	23	0	0	0	0	2	0	0	0	0	0	0	0	0	27	1	0	0	0
FLAX.D	0	25	0	0	0	0	1	0	0	0	0	0	0	0	0	34	0	0	0	0
FLAX.E	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	23	4	1	0	0
FLAX.F	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
SI-A	0	0	4	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	5	4
SI-B	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	18	2
SI-C	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	4	0
SI-D	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	11	6
SI-E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0
SI-F	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	5	0
SII-A	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	170	0
SII-B	0	0	0	0	0	0	2	0	0	1	0	0	0	0	3	0	0	0	171	0
SII-C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	0
SII-D	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	48	0
FLAX.A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	11	0
FLAX.B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	17	0
FLAX.C	0	0	0	0	0	0	1	0	0	0	0	0	0	0	11	0	0	0	19	0
FLAX.D	0	0	0	0	0	0	2	0	0	0	0	1	0	0	7	0	0	0	15	0
FLAX.E	0	0	0	0	0	0	0	0	0	0	1	0	1	0	5	0	0	0	17	0
FLAX.F	0	0	0	0	0	0	2	0	0	0	0	0	0	0	7	0	0	0	17	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
SI-A	0	0	32	0	0	0	0	0	13	0	1	0	0	2	2	0	0	0	0	0
SI-B	0	0	11	0	0	0	0	0	64	0	0	0	0	5	2	0	39	0	0	0
SI-C	0	0	22	3	0	0	0	0	6	0	0	0	0	9	5	0	2	0	0	0
SI-D	0	0	25	0	0	2	0	0	10	0	0	0	0	8	17	0	20	0	0	0
SI-E	0	0	41	0	0	1	0	0	126	0	1	0	0	0	2	0	34	0	0	0
SI-F	0	0	12	2	0	0	0	0	0	0	0	0	0	13	8	0	4	0	0	0
SII-A	0	0	3	0	0	3	0	0	4	0	0	0	0	2	0	0	6	0	0	0
SII-B	0	0	19	0	0	0	0	0	11	0	0	0	2	7	3	0	9	0	0	0
SII-C	0	0	0	0	0	0	0	0	2	0	0	0	1	0	2	0	7	0	0	0
SII-D	0	0	1	0	0	2	0	0	48	0	0	0	0	2	2	0	7	0	0	0
FLAX.A	0	0	0	0	0	0	0	0	2	0	0	0	3	20	0	0	0	0	0	0
FLAX.B	0	0	1	0	0	6	0	0	6	0	1	0	0	0	11	0	1	0	0	0
FLAX.C	0	0	8	0	0	2	0	0	6	0	0	0	0	0	19	0	5	0	0	0
FLAX.D	0	0	5	0	0	0	0	0	14	0	0	0	0	2	8	0	1	0	0	0
FLAX.E	0	0	3	0	0	1	0	0	3	0	0	0	0	0	1	0	1	0	0	0
FLAX.F	0	0	2	0	0	0	0	0	1	0	0	0	0	0	11	0	5	0	0	0

	TRIL		DRAP		DISC		UNWN														
SI-A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SI-B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SI-C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SI-D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SI-E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SI-F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SII-A	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SII-B	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SII-C	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SII-D	0	0	0	0	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FLAX.F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

HARIHARI MODERN SAMPLES

(SNAKE CREEK, HARIHARI, EVANS ROAD)

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
SNAK.A	12	74	0	0	17	3	1	10	1	8	0	0	0	3	14	5	14	7	0	0
SNAK.B	14	322	0	0	11	4	0	2	0	3	0	0	0	0	6	1	0	0	0	0
SNAK.C	26	47	3	0	23	2	0	15	0	1	0	0	0	0	15	6	0	3	0	0
SNAK.D	17	20	1	0	1	3	0	4	0	0	0	0	0	0	4	12	1	4	0	0
SNAK.E	1	418	0	0	3	1	0	8	0	0	0	0	0	0	4	1	0	2	0	0
SNAK.F	33	72	0	0	15	3	0	3	0	2	0	1	0	2	11	3	3	4	0	0
HARI.A	3	48	0	1	57	2	0	2	19	2	0	1	0	2	51	0	1	1	0	0
HARI.B	0	54	0	0	54	3	0	2	13	3	0	0	0	1	50	1	0	0	0	0
HARI.C	1	50	3	0	80	7	0	2	22	2	0	0	0	1	25	0	0	0	0	0
HARI.D	0	52	0	0	51	2	0	1	11	1	0	0	0	0	22	1	0	2	0	0
HARI.E	3	62	0	0	27	3	0	0	7	1	1	0	0	3	41	0	0	3	0	0
HARI.F	1	63	1	0	65	3	1	2	11	5	1	0	0	1	42	0	2	4	0	0
EVAN.A	125	40	23	7	24	0	0	21	0	7	0	0	0	1	9	3	0	20	5	0
EVAN.B	146	6	3	0	6	0	0	82	0	0	0	0	0	0	4	2	7	2	0	0
EVAN.C	33	6	1	1	0	0	0	23	0	3	0	0	0	2	8	123	0	7	0	0
EVAN.D	19	4	3	0	2	0	0	12	0	1	0	0	0	0	2	6	1	7	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COPR	CRAR	DRPH	MYRS	HEBE
SNAK.A	12	0	0	0	0	0	9	0	171	20	0	0	7	0	1	34	1	0	1	0
SNAK.B	0	0	0	0	0	0	3	0	39	5	0	0	1	0	0	15	3	0	1	0
SNAK.C	0	0	0	0	0	0	62	0	201	21	0	0	4	0	0	24	1	0	0	0
SNAK.D	1	0	1	0	0	0	32	0	228	21	0	0	0	0	0	17	0	0	4	0
SNAK.E	0	2	0	0	0	0	31	0	119	9	0	0	2	0	0	17	1	0	0	0
SNAK.F	0	0	0	0	0	0	8	0	164	13	0	0	2	1	0	15	0	0	3	0
HARI.A	0	0	2	0	0	0	29	0	20	3	1	0	20	1	0	7	0	0	3	0
HARI.B	0	0	0	0	0	0	81	0	26	3	0	2	14	0	0	6	0	0	1	0
HARI.C	0	0	0	0	0	0	54	0	39	2	0	0	19	0	0	7	1	0	1	0
HARI.D	0	0	0	0	0	0	78	0	23	2	0	0	8	0	0	2	0	0	1	0
HARI.E	0	1	0	0	0	0	50	0	14	3	0	0	16	0	0	5	0	0	1	0
HARI.F	0	1	0	0	0	0	36	0	11	2	2	0	20	1	0	5	0	0	1	0
EVAN.A	0	0	0	0	0	0	1	0	54	10	0	1	3	4	0	48	0	0	5	0
EVAN.B	0	0	0	0	0	0	2	0	14	4	0	0	4	0	0	21	0	0	3	0
EVAN.C	0	0	18	0	0	0	5	0	26	0	0	0	0	0	0	2	0	0	4	0
EVAN.D	0	0	6	1	0	0	1	0	10	0	0	0	0	0	0	26	0	0	4	0

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
SNAK.A	0	5	0	0	0	0	2	0	0	0	0	1	0	0	0	35	1	2	0	0
SNAK.B	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	1	0	0
SNAK.C	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	0
SNAK.D	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0
SNAK.E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0
SNAK.F	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	27	0	1	0	0
HARI.A	0	5	0	0	0	0	0	1	0	1	0	1	0	0	0	29	0	1	0	0
HARI.B	0	2	0	0	0	0	0	0	0	0	0	1	6	0	0	6	0	1	0	0
HARI.C	0	4	0	0	0	0	0	0	0	0	0	0	101	0	0	6	1	0	0	0
HARI.D	0	1	0	0	0	0	0	0	0	0	0	1	4	0	0	15	2	0	0	0
HARI.E	0	2	0	0	0	0	0	0	0	0	0	0	7	0	0	14	0	1	0	0
HARI.F	0	4	0	0	0	0	1	0	0	0	0	0	5	0	0	23	0	0	0	1
EVAN.A	0	4	0	0	0	0	115	0	0	0	0	9	0	0	0	61	6	1	0	0
EVAN.B	0	1	0	0	0	0	77	0	0	0	0	0	0	0	0	44	9	0	0	0
EVAN.C	0	0	0	0	0	0	107	0	0	0	0	37	0	0	0	113	6	0	0	0
EVAN.D	0	2	0	0	0	0	128	0	0	0	0	0	0	0	0	53	3	3	0	0

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
SNAK.A	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	137	0
SNAK.B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	121	0
SNAK.C	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	61	0
SNAK.D	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	71	0
SNAK.E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	173	0
SNAK.F	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	143	1
HARI.A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	0
HARI.B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	0
HARI.C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0
HARI.D	0	0	1	0	0	2	0	0	0	0	0	1	0	0	2	0	0	0	43	0
HARI.E	0	0	1	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	62	0
HARI.F	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	83	0
EVAN.A	0	0	4	0	9	0	0	0	0	0	0	0	3	0	1	0	0	0	11	0
EVAN.B	0	0	5	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	3	6
EVAN.C	0	0	7	0	0	0	0	0	0	0	1	0	0	0	7	0	0	0	8	0
EVAN.D	0	0	0	0	0	0	0	0	0	0	1	0	0	0	8	0	0	0	0	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
SNAK.A	0	0	8	0	0	6	0	0	3	0	2	0	14	5	0	0	3	0	0	0
SNAK.B	0	0	21	0	0	5	0	0	14	0	3	0	8	0	10	0	2	0	0	0
SNAK.C	0	0	18	0	0	1	0	0	84	0	0	0	2	5	5	0	0	0	0	0
SNAK.D	0	0	21	0	0	0	0	0	134	0	0	0	1	3	4	0	0	0	0	0
SNAK.E	0	0	12	0	0	0	0	0	19	0	0	0	6	0	2	0	11	0	0	0
SNAK.F	0	0	52	0	0	5	0	0	19	0	0	0	3	8	0	0	8	0	0	0
HARI.A	0	0	11	0	0	6	0	0	4	0	0	0	4	0	6	0	12	0	0	0
HARI.B	0	0	4	0	0	9	0	0	1	0	0	0	2	0	6	0	5	0	0	0
HARI.C	0	0	7	0	0	1	0	0	0	0	0	0	0	0	3	0	12	0	0	0
HARI.D	0	0	5	0	0	5	0	0	2	0	0	0	3	0	5	0	14	0	0	0
HARI.E	0	0	7	0	0	0	0	0	5	0	0	0	2	0	7	0	25	0	0	0
HARI.F	0	0	11	0	0	3	0	0	4	0	0	0	6	0	9	0	16	0	0	0
EVAN.A	0	0	1	0	0	1	0	0	6	0	0	0	0	2	1	0	5	0	0	0
EVAN.B	0	0	1	1	0	0	0	0	1	0	0	0	0	0	94	0	0	0	0	0
EVAN.C	0	0	1	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0
EVAN.D	0	0	1	0	0	2	0	0	5	0	0	3	0	0	2	0	0	0	0	0

	TRIL	DRAP	DISC	UNWN																
SNAK.A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SNAK.B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SNAK.C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SNAK.D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SNAK.E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SNAK.F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.B	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.D	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HARI.F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EVAN.A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EVAN.B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EVAN.C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EVAN.D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

OTHER SOUTH ISLAND MODERN SAMPLES

(MT.RAK = MOUNT RAKEAHUA
TAB.HL = TABLE HILL)

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
MOAST1	2	23	0	19	8	2	0	0	14	105	0	15	0	0	0	0	3	2	0	0
MOAST2	1	4	0	11	2	0	0	0	2	23	0	1	0	0	0	0	2	1	0	0
MOAST3	0	5	0	15	0	0	0	0	5	20	1	0	0	0	0	2	5	12	0	0
MOAST4	0	5	0	95	1	0	0	0	20	27	1	1	0	0	3	0	3	197	0	0
MOAST5	4	13	0	21	8	3	0	0	14	60	2	11	0	0	0	8	1	11	0	0
NTHST	7	7	0	37	9	5	0	0	12	42	0	6	2	0	0	0	3	10	0	0
MOAST6	0	5	0	4	2	0	0	0	1	192	0	1	2	0	0	1	1	1	0	0
KIWIFT	0	8	0	12	3	1	0	0	3	100	0	3	4	0	0	0	3	0	0	0
FANGST	1	5	0	11	5	1	0	0	83	49	0	7	1	0	0	0	4	7	0	0
WILBFN	0	5	0	8	5	1	0	0	0	11	0	7	0	0	0	0	0	6	0	0
KR 1	0	22	1	6	24	6	0	0	20	34	1	3	2	0	17	16	1	5	0	0
KR 2	1	9	0	19	21	5	0	0	3	35	0	3	0	0	15	15	5	49	0	0
MKB-B	0	20	1	90	6	3	0	0	8	6	0	10	1	0	1	0	0	0	0	0
MKB-T	1	51	1	7	25	11	0	0	51	20	0	8	0	0	2	4	2	4	0	0
MT.RAK	1	139	0	14	65	8	0	0	11	47	18	5	3	3	0	1	2	1	0	0
TAB.HL	1	118	0	4	74	16	0	0	61	120	25	5	1	2	0	5	3	2	0	0
AH-CB	2	23	0	19	8	9	0	0	1	24	31	40	0	0	1	3	0	1	0	0
AH-FH	5	58	0	4	11	44	0	0	5	22	22	16	0	0	2	2	0	0	0	0
AH-SW1	1	26	0	9	9	8	0	0	3	24	30	36	0	0	2	3	2	2	0	0
AH-SW2	1	21	0	31	5	5	0	0	2	28	28	16	0	1	1	7	0	1	0	0
AH-SW3	1	20	0	24	3	8	0	0	3	20	18	8	0	2	0	3	0	4	0	0
OMANS1	1	0	1	7	3	0	0	0	8	204	31	48	1	0	0	0	2	3	0	0
OMANS2	1	0	1	0	0	1	0	0	1	27	3	21	1	0	0	0	0	2	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COPR	CRAR	DRPH	MYRS	HEBE
MOAST1	0	0	0	0	0	0	4	0	0	2	0	0	0	192	1	19	0	2	2	2
MOAST2	0	0	0	0	0	0	6	0	0	1	0	0	0	3	0	27	0	4	4	5
MOAST3	0	0	0	0	0	0	4	0	0	7	0	0	0	10	2	40	0	1	2	6
MOAST4	0	0	0	0	0	0	3	0	0	58	0	0	0	9	0	40	0	21	36	1
MOAST5	0	0	0	0	0	0	3	0	1	2	0	0	0	90	1	35	0	2	2	4
NTHST	0	0	0	0	0	0	3	0	0	9	0	0	0	6	0	91	0	2	5	15
MOAST6	0	0	0	0	0	0	0	0	0	8	0	0	0	34	0	10	0	0	1	5
KIWIFT	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0	12	0	0	2	4
FANGST	0	0	0	0	0	0	2	0	1	6	0	0	0	12	0	127	0	0	2	3
WILBFN	0	0	0	0	0	0	1	0	0	1	0	0	0	8	3	21	0	0	1	5
KR 1	0	0	0	0	0	0	31	0	21	1	0	0	1	3	2	12	0	0	3	0
KR 2	0	0	0	0	0	0	20	0	12	2	0	0	1	2	1	23	0	2	5	0
MKB-B	0	0	0	0	0	0	2	0	1	0	0	0	0	7	1	54	5	1	1	0
MKB-T	0	0	0	0	0	0	7	0	2	0	0	0	7	10	3	42	13	4	2	0
MT.RAK	0	0	0	0	0	0	0	0	3	1	0	0	0	14	1	16	1	0	5	0
TAB.HL	0	0	0	0	0	0	4	0	6	3	0	0	1	37	0	50	2	3	3	0
AH-CB	0	0	1	0	0	4	4	0	2	1	0	0	0	1	2	16	0	1	3	2
AH-FH	1	0	0	0	0	0	2	0	4	1	0	0	1	6	1	8	0	12	5	0
AH-SW1	1	0	0	0	0	0	18	0	4	2	0	0	0	2	0	6	1	19	1	3
AH-SW2	1	0	3	0	0	0	8	0	8	2	0	0	0	3	0	22	1	7	11	0
AH-SW3	1	0	1	0	0	0	4	0	4	3	0	0	0	2	0	28	3	35	10	2
OMANS1	0	0	0	0	0	0	0	0	0	0	0	0	0	7	2	6	0	4	0	2
OMANS2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	11	14	1	1	1	3

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
MOAST1	1	61	2	0	27	0	0	3	0	1	6	0	0	0	0	87	0	0	0	1
MOAST2	0	213	0	0	6	0	0	3	0	0	56	0	0	0	0	172	0	0	0	3
MOAST3	0	66	0	0	2	0	0	2	0	1	581	0	0	0	0	82	0	0	0	11
MOAST4	0	516	0	0	21	0	0	0	0	0	14	0	0	0	0	31	1	0	0	7
MOAST5	0	139	0	0	13	0	0	0	0	2	3	0	0	0	8	102	3	0	0	1
NTHST	0	87	0	0	10	0	0	1	1	0	882	0	0	0	0	112	0	0	0	12
MOAST6	0	7	0	0	2	0	0	1	0	2	0	0	0	0	0	84	1	0	0	1
KIWIFT	0	35	0	0	0	0	3	1	4	2	0	0	0	0	0	603	0	0	0	16
FANGST	0	100	0	0	1	0	0	0	2	4	1	0	0	0	0	776	0	0	0	11
WILBFN	0	16	0	0	1	0	2	0	0	4	3	0	0	0	0	530	0	0	0	49
KR 1	0	603	0	0	60	0	0	0	1	0	0	0	0	0	0	35	0	0	0	2
KR 2	0	203	0	0	76	0	3	0	0	1	0	0	0	0	0	32	1	0	0	2
MKB-B	0	52	0	0	6	0	0	2	1	0	1	0	0	0	0	65	2	0	0	10
MKB-T	0	115	5	0	6	0	1	1	6	5	2	0	0	0	0	105	3	0	0	30
MT.RAK	0	2	6	0	12	0	37	2	1	1	0	0	0	0	0	36	8	0	0	11
TAB.HL	0	4	28	0	12	0	2	2	1	2	0	0	0	0	0	59	7	0	0	38
AH-CB	0	5	0	0	1	0	3	0	0	0	5	0	0	0	0	74	0	0	0	14
AH-FH	2	12	0	0	38	0	0	0	0	1	0	0	0	0	0	48	1	0	0	5
AH-SW1	0	11	0	0	4	0	1	2	1	0	0	0	0	0	1	63	1	0	0	4
AH-SW2	0	19	2	0	2	0	3	0	2	1	1	0	0	0	0	70	0	0	0	3
AH-SW3	2	13	0	0	10	0	3	2	0	0	0	0	0	0	0	74	1	0	0	2
OMANS1	0	2	0	4	0	0	1	7	0	1	0	0	0	0	0	392	0	0	0	7
OMANS2	0	12	0	6	0	1	0	6	0	4	0	0	0	0	0	587	0	0	0	19

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
MOAST1	0	0	2	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	5	0
MOAST2	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
MOAST3	0	0	1	15	0	0	0	0	0	3	0	0	4	0	0	0	0	0	2	0
MOAST4	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	11	0
MOAST5	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0
NTHST	0	0	1	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	3	0
MOAST6	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
KIWIFT	0	21	0	6	0	0	0	0	0	0	0	45	0	0	0	0	0	0	4	0
FANGST	0	0	34	12	8	0	0	0	0	0	0	0	1	0	2	0	0	0	2	0
WILBFN	0	0	10	1	0	0	2	0	0	0	0	0	2	0	0	0	0	0	4	0
KR 1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	0	0	11	0
KR 2	0	0	2	3	0	0	0	0	0	0	0	1	7	0	0	0	0	0	9	0
MKB-B	0	0	0	0	1	0	0	0	0	0	1	0	1	0	31	0	0	0	0	0
MKB-T	0	0	2	7	3	0	0	0	0	0	52	2	2	1	179	0	0	0	16	0
MT.RAK	0	0	0	1	0	0	0	4	0	0	0	1	0	0	9	0	0	0	8	0
TAB.HL	0	0	0	0	0	0	0	0	0	0	1	0	0	0	6	0	0	0	11	0
AH-CB	0	9	2	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	13	0
AH-FH	0	1	1	1	0	0	2	0	0	0	0	1	1	0	3	0	0	0	19	0
AH-SW1	0	2	0	4	0	0	0	0	0	0	0	0	2	0	13	0	0	0	15	0
AH-SW2	0	1	0	4	2	0	4	1	0	0	0	1	0	0	6	0	0	0	7	0
AH-SW3	0	0	1	3	0	0	0	0	0	1	0	0	1	0	2	0	0	0	11	0
OMANS1	0	2	3	7	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	0
OMANS2	0	2	114	38	6	0	0	0	0	0	1	0	0	0	44	0	0	0	1	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
MOAST1	0	0	2	0	6	5	0	0	0	0	0	2	0	18	0	0	41	0	0	0
MOAST2	0	0	0	0	0	3	0	0	0	0	0	0	0	4	0	0	19	0	0	0
MOAST3	0	0	0	0	1	4	0	0	0	0	0	0	0	14	0	0	112	0	0	13
MOAST4	0	0	0	0	0	3	0	0	0	0	5	0	0	4	5	0	46	0	0	0
MOAST5	0	0	0	0	0	0	22	0	0	0	0	0	0	8	0	0	21	0	0	4
NTHST	0	0	4	0	0	3	0	0	1	0	0	0	0	20	2	0	30	0	0	2
MOAST6	0	0	1	0	0	3	0	0	1	0	0	0	7	0	2	0	12	0	0	1
KIWIFT	0	0	1	0	0	75	16	0	2	0	0	0	0	0	1	0	17	0	0	0
FANGST	0	0	1	0	0	7	0	0	1	0	0	0	1	0	0	0	45	0	0	0
WILBFN	0	0	0	0	0	9	2	0	0	0	0	0	0	0	0	0	33	0	0	5
KR 1	0	1	1	0	1	2	1	0	0	0	0	0	2	0	1	0	6	0	0	0
KR 2	0	0	4	0	1	1	0	0	0	0	0	0	0	0	0	0	7	0	0	0
MKB-B	0	0	0	0	0	2	1	2	0	0	0	0	0	2	0	0	18	0	0	1
MKB-T	0	1	7	0	3	3	1	1	0	1	0	1	0	0	0	0	33	0	0	1
MT.RAK	0	1	9	0	0	0	0	1	1	0	0	0	0	0	2	0	12	0	0	0
TAB.HL	0	0	5	0	0	1	0	0	2	0	0	0	0	0	0	0	10	0	0	0
AH-CB	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	41	13	0	0	0
AH-FH	0	0	2	0	0	0	0	0	2	0	0	0	1	0	4	1	9	0	0	0
AH-SW1	0	0	3	0	0	4	0	0	2	0	0	0	0	0	1	0	9	0	0	5
AH-SW2	0	2	4	0	0	0	1	0	0	0	0	0	1	0	13	0	19	0	0	0
AH-SW3	1	0	7	0	0	0	2	0	2	0	0	0	4	2	2	0	7	0	0	3
OMANS1	0	0	2	0	10	0	5	0	1	0	0	0	7	0	0	0	12	0	0	0
OMANS2	0	1	1	0	8	0	4	0	1	0	0	2	1	1	0	0	10	0	0	0

	TRIL	DRAP	DISC	UNWN																
MOAST1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOAST2	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOAST3	0	0	3	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOAST4	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOAST5	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NTHST	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOAST6	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KIWIFT	0	0	0	9	37	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FANGST	0	0	0	1	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WILBFN	0	0	0	0	218	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KR 1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KR 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MKB-B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MKB-T	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MT.RAK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAB.HL	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AH-CB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AH-FH	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AH-SW1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AH-SW2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AH-SW3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OMANS1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OMANS2	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

LADY LAKE MODERN SAMPLES

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
PHA	16	23	0	0	20	2	0	1	0	8	0	0	0	1	18	1	1	0	0	0
PHB	4	34	0	0	12	1	0	0	0	5	0	0	0	0	98	5	3	1	0	0
PHC	5	69	0	0	7	0	0	0	0	7	0	0	0	0	40	3	0	1	0	0
DDD	28	108	1	0	28	0	0	0	0	21	0	0	0	0	13	2	0	0	0	0
PHE	21	61	0	0	13	0	0	0	0	7	0	0	0	1	70	2	0	2	0	0
PHF	11	56	5	1	34	3	0	0	50	9	0	0	0	0	94	3	1	0	0	0
S-1	13	112	3	4	18	2	0	0	10	18	1	0	0	0	20	11	0	4	0	0
S-2	3	82	0	2	22	6	0	0	1	15	0	0	0	1	33	9	0	10	4	0
S-3	1	69	1	0	23	4	0	0	0	9	0	0	0	0	30	9	6	2	0	1
S-4	4	66	0	1	28	5	2	0	0	17	1	2	0	1	48	10	0	4	2	0
S-5	4	74	0	0	39	3	0	0	1	20	0	0	0	0	46	5	5	6	1	2
S-6	11	94	0	2	8	1	0	0	15	20	0	0	0	0	25	11	1	5	0	0
S-7	2	73	0	0	12	5	0	0	0	22	2	1	0	0	57	3	1	0	0	0
S-8	5	65	0	0	19	5	0	0	0	17	0	2	0	1	70	3	0	4	0	0
S-9	0	13	1	2	3	0	0	0	3	6	0	0	0	0	27	8	0	2	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COFR	CRAR	DRPH	MYRS	HEBE
PHA	0	0	0	0	0	0	18	3	86	1	0	0	2	0	0	3	0	0	7	0
PHB	0	0	0	0	0	0	7	2	67	14	0	0	1	0	0	5	1	0	10	0
PHC	0	1	0	0	0	0	9	3	48	4	0	0	1	0	0	9	1	0	1	0
DDD	0	0	3	0	0	0	11	6	15	0	0	0	1	2	0	26	0	0	1	0
PHE	1	0	0	0	0	0	6	9	25	2	0	0	0	0	1	15	0	0	3	0
PHF	0	0	0	0	0	0	1	2	13	4	0	0	1	0	0	6	0	0	1	0
S-1	0	0	0	0	0	0	6	9	21	2	0	0	3	1	0	11	0	0	7	0
S-2	1	0	2	0	0	0	8	11	33	4	0	0	2	1	0	6	0	0	1	0
S-3	0	1	1	0	0	0	21	12	34	6	0	0	1	1	0	8	0	0	5	0
S-4	1	1	5	0	0	0	17	12	55	5	0	0	5	2	0	20	0	1	3	0
S-5	0	0	4	0	0	0	15	10	37	8	0	0	0	0	0	8	0	0	7	0
S-6	0	0	0	0	0	0	10	5	13	1	0	0	1	2	0	12	0	0	3	0
S-7	0	0	3	0	0	0	27	12	44	3	0	0	2	1	0	18	0	0	9	0
S-8	1	0	1	0	0	0	16	13	50	2	0	0	1	0	0	13	0	0	6	0
S-9	1	0	2	0	0	0	21	3	24	3	0	0	2	1	1	10	0	0	0	0

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
PHA	0	3	0	0	0	0	0	0	0	0	0	0	2	0	0	25	2	1	0	0
PHB	0	4	0	0	0	0	0	0	0	0	0	0	2	0	0	23	1	3	0	0
PHC	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	21	0	0	0	0
DDD	0	12	0	0	0	0	1	0	0	0	0	0	2	0	0	17	0	0	0	1
PHE	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	1
PHF	0	12	0	0	0	0	0	0	0	0	0	0	2	0	0	9	0	0	0	0
S-1	0	5	0	0	0	0	1	0	0	0	0	0	0	0	0	19	0	0	0	3
S-2	0	10	0	0	0	0	3	0	0	0	0	0	0	0	0	19	3	0	0	4
S-3	0	10	0	0	1	0	0	0	0	0	0	0	0	0	0	9	0	1	0	0
S-4	0	16	0	0	0	0	0	0	0	0	0	1	1	0	0	22	0	2	0	0
S-5	0	3	0	0	0	0	1	0	0	0	0	1	0	0	0	17	1	2	0	1
S-6	0	12	0	0	0	0	5	0	0	0	0	0	0	0	0	14	0	0	0	5
S-7	0	10	0	0	0	0	0	0	0	0	0	0	2	0	0	19	0	2	0	0
S-8	0	12	0	0	0	0	1	0	0	0	0	0	2	0	0	11	0	0	0	0
S-9	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	2

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
PHA	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	60	0
PHB	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	4	0
PHC	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	0	0	0	8	0
DDD	0	0	0	0	0	0	0	0	0	0	0	0	1	3	51	0	0	0	8	0
PHE	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	3	0
PHF	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	0	0	0	4	0
S-1	0	0	0	0	0	0	0	0	0	3	0	0	1	0	22	0	0	0	10	0
S-2	0	0	0	0	1	0	3	0	0	3	0	0	0	3	5	0	0	0	65	0
S-3	0	0	1	0	0	0	1	0	0	4	0	0	1	6	6	0	0	0	47	0
S-4	0	0	0	3	0	0	4	0	0	2	0	0	1	0	5	0	0	0	52	0
S-5	0	0	0	0	0	0	1	0	0	0	0	0	1	10	8	0	0	0	64	0
S-6	0	0	0	2	2	0	0	0	0	4	0	0	0	0	11	0	0	0	36	0
S-7	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	0	0	52	0
S-8	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0	0	0	47	0
S-9	0	0	0	1	0	0	0	0	0	3	0	0	1	2	16	0	0	0	30	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
PHA	0	0	14	0	0	0	0	0	2	0	0	0	1	0	2	0	18	0	0	5
PHB	0	0	0	0	0	0	0	0	1	0	0	0	1	0	4	0	10	0	0	2
PHC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	10	0	0	0
DID	0	0	3	0	0	0	0	0	1	0	0	0	0	0	2	0	4	0	0	0
PHE	0	0	3	0	0	0	0	0	0	0	0	2	0	1	2	0	2	0	0	0
PHF	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	11	0	0	0
S-1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	21	0	0	0
S-2	0	0	10	0	0	0	0	0	1	0	0	2	1	0	6	0	17	0	0	2
S-3	0	0	5	0	0	3	0	0	1	0	0	0	0	0	3	0	12	0	0	2
S-4	0	0	5	0	0	0	0	0	1	0	0	1	0	0	5	0	14	0	0	3
S-5	0	0	7	0	0	2	0	0	0	0	0	0	1	0	2	0	24	0	0	1
S-6	0	0	3	0	0	1	0	0	1	0	0	0	0	0	2	0	6	0	0	1
S-7	0	0	7	0	0	2	0	0	1	0	0	2	0	0	2	0	20	0	0	1
S-8	0	0	6	0	0	4	0	0	1	0	0	0	0	0	11	0	20	0	0	0
S-9	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0

	TRIL		DRAP		DISC	UNWN														
PHA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DDD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-2	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-3	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-4	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-5	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-6	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-8	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S-9	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

LADY LAKE FOSSIL SAMPLES

DEPTH 0-382 cm

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
SURFS	18	34	3	0	5	0	0	0	0	7	1	0	0	1	3	2	1	2	0	0
10-12	16	31	10	4	3	0	0	0	2	6	1	2	0	1	8	17	0	1	0	1
20-22	3	53	0	0	1	1	0	0	0	2	1	1	0	0	10	5	0	4	0	0
60-62	8	105	6	1	8	0	2	0	5	10	0	0	0	0	24	7	0	2	0	1
98-100	11	98	2	1	3	1	0	0	1	15	0	0	0	0	11	10	2	1	0	1
120-22	8	111	1	0	14	2	1	0	0	9	1	0	0	0	15	14	0	3	0	0
148-50	8	119	3	0	7	4	0	0	0	9	3	0	0	0	13	19	0	1	0	0
160-62	4	77	1	0	2	4	0	0	0	8	0	0	0	0	16	6	0	1	0	0
180-82	11	64	0	0	8	1	0	0	0	8	0	0	0	0	9	5	0	3	0	0
198-20	11	58	0	0	8	3	0	0	0	6	0	0	0	0	6	2	0	1	0	0
220-22	6	45	2	0	5	1	0	0	0	10	0	0	0	0	11	10	0	2	0	0
240-42	8	65	0	0	8	3	1	0	0	4	0	0	0	0	11	8	0	1	0	1
260-62	3	75	2	0	12	3	1	0	0	12	1	0	5	0	16	7	0	3	0	0
280-82	14	129	2	1	17	8	0	0	0	13	2	0	0	0	11	5	0	3	0	0
290-92	16	119	3	0	15	5	2	0	0	13	3	0	0	0	10	2	0	4	0	0
310-12	11	100	1	0	6	2	1	0	0	11	3	0	0	1	12	10	0	4	0	0
320-22	12	141	4	0	26	7	2	0	0	13	3	0	0	0	10	9	0	1	0	0
340-42	11	112	2	0	18	4	1	0	0	17	2	0	0	0	10	8	0	3	0	0
360-62	14	126	8	0	34	6	0	0	0	6	2	0	0	0	4	4	0	1	0	0
380-82	8	149	5	0	33	5	3	0	0	8	0	0	0	2	1	4	0	0	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COPR	CRAR	DRPH	MYRS	HEBE
SURFS	0	0	0	0	0	0	1	1	5	3	0	0	0	0	0	28	0	0	4	0
10-12	0	0	0	0	0	0	7	1	17	2	0	0	4	0	0	18	0	0	4	0
20-22	0	0	3	0	0	0	4	2	17	0	0	0	0	0	0	2	0	0	1	0
60-62	0	0	0	0	0	0	8	5	16	1	0	0	2	1	1	4	0	0	1	0
98-100	0	0	0	0	0	0	8	0	19	0	0	0	2	0	0	3	0	0	3	0
120-22	0	0	0	0	0	0	7	0	24	0	0	0	2	0	0	5	0	0	3	0
148-50	0	0	0	0	0	0	8	1	38	1	0	0	3	2	0	5	0	0	0	0
160-62	0	0	0	0	0	0	1	9	20	0	0	0	0	1	0	3	0	0	3	0
180-82	0	0	3	0	0	0	0	9	22	0	0	0	0	0	0	2	0	0	5	0
198-20	0	0	0	0	0	0	0	3	16	0	0	0	0	2	0	5	0	0	5	0
220-22	0	0	0	0	0	0	1	5	24	0	0	0	0	1	0	3	0	0	1	0
240-42	0	0	2	0	0	0	0	2	10	2	0	0	0	0	0	4	0	0	3	0
260-62	0	0	0	0	0	0	7	2	25	0	0	0	5	2	0	3	0	0	0	0
280-82	0	0	0	0	0	0	11	0	13	1	0	0	3	1	0	8	0	0	5	0
290-92	0	0	0	0	0	0	8	1	15	3	0	0	2	1	0	13	0	0	2	0
310-12	0	0	0	1	0	0	6	0	25	2	0	0	8	1	0	11	0	0	1	0
320-22	0	0	0	0	0	0	9	2	15	0	0	0	3	1	0	8	0	0	5	0
340-42	0	0	0	0	0	0	10	3	21	2	0	0	4	2	0	26	0	0	1	0
360-62	0	0	0	0	0	0	4	0	17	0	0	0	6	1	2	2	0	0	3	0
380-82	0	0	0	0	0	0	4	1	19	1	0	0	2	0	0	5	0	0	3	0

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
SURFS	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	9	0	0	0	0
10-12	0	3	0	2	0	0	1	0	0	0	0	0	0	0	0	52	0	0	0	2
20-22	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	22	0	0	0	0
60-62	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	17	0	0	0	0
98-100	0	5	0	0	0	0	3	0	0	0	0	0	1	0	0	32	0	0	0	1
120-22	0	6	0	0	0	0	3	0	0	0	0	0	0	0	0	9	0	0	0	0
148-50	0	1	0	0	0	0	8	0	0	1	0	0	1	0	0	12	0	0	0	0
160-62	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0	0	0
180-82	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	9	0	0	0	0
198-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1
220-22	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	4	0	0	0	0
240-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
260-62	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	4	0	0	0	0
280-82	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
290-92	0	6	0	1	0	0	3	0	0	0	0	0	0	0	0	7	0	0	0	0
310-12	0	2	0	0	0	0	3	0	0	0	0	0	0	0	0	6	0	0	0	1
320-22	0	1	0	1	0	0	5	0	0	0	0	0	0	0	0	8	0	0	0	0
340-42	0	2	0	0	0	0	3	0	0	0	0	0	0	0	0	4	0	0	0	0
360-62	0	3	0	2	0	0	2	0	0	0	0	0	0	0	0	9	1	0	0	2
380-82	0	0	0	3	0	0	2	0	0	0	0	0	1	0	0	6	0	0	0	0

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
SURFS	0	0	2	0	0	0	0	6	0	0	0	0	0	0	25	0	0	0	21	0
10-12	0	0	0	0	0	0	0	0	0	0	0	0	1	2	12	0	0	0	46	0
20-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	5	0
60-62	0	0	0	0	0	0	0	0	0	1	0	0	0	1	8	0	0	0	21	0
98-100	0	0	0	0	0	0	0	0	0	5	0	0	3	1	9	0	0	0	8	0
120-22	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5	0	0	0	29	0
148-50	0	0	0	1	0	0	0	0	0	1	0	0	3	0	6	0	0	0	19	0
160-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0
180-82	0	0	0	0	0	0	0	0	0	0	3	0	0	0	5	0	0	0	8	0
198-20	0	0	0	0	0	0	0	0	0	0	1	0	0	1	5	0	0	0	13	0
220-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	4	0
240-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	2	0
260-62	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	22	0
280-82	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	0	0	0	31	0
290-92	0	0	0	0	0	0	0	0	0	1	0	0	0	2	5	0	0	0	15	0
310-12	0	0	0	2	0	0	2	0	0	3	0	0	0	0	7	0	0	0	28	0
320-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	31	0
340-42	0	0	0	0	0	0	2	0	0	1	0	0	0	0	6	0	0	0	7	0
360-62	0	0	0	2	0	0	0	0	0	0	0	0	0	0	7	0	0	0	44	0
380-82	0	0	0	0	0	0	1	0	0	3	0	0	1	0	6	0	0	0	79	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
SURFS	0	0	13	0	7	0	0	0	1	0	0	0	0	0	0	0	6	0	0	0
10-12	0	0	19	0	0	5	0	0	0	0	0	0	0	0	1	0	15	0	0	0
20-22	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	9	0	0	0
60-62	0	0	2	0	0	2	0	0	1	0	0	0	0	0	1	0	8	0	0	0
98-100	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	21	0	0	0
120-22	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	12	0	0	0
148-50	0	0	5	0	0	1	0	0	0	0	0	0	0	0	2	0	10	0	0	0
160-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0
180-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
198-20	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
220-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
240-42	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0
260-62	0	0	2	0	0	3	0	0	0	0	0	0	0	0	2	0	3	0	0	0
280-82	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0	0	0
290-92	0	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
310-12	0	0	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
320-22	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0
340-42	0	0	3	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	0
360-62	0	0	6	0	0	1	0	0	0	0	0	0	0	0	0	0	8	0	0	0
380-82	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0

			TRIL			DRAP			DISC			UNWN									
SURFS	0	0	7	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10-12	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20-22	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60-62	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98-100	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
120-22	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148-50	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
160-62	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
180-82	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
198-20	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
220-22	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
240-42	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
260-62	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
280-82	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
290-92	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
310-12	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
320-22	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
340-42	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
360-62	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
380-82	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

LADY LAKE FOSSIL SAMPLES

DEPTH 398-705 cm

	DACP	D.CU	D.CO	LIBO	P.FE	P.SP	P.TO	P.WA	P.HA	N.FU	N.ME	PINE	MYRT	CARP	QUIN	ELAE	ARIS	PSEP	PITT	FUCH
398-40	8	174	5	0	52	10	0	0	0	5	1	0	1	0	2	3	0	4	0	1
420-22	5	129	1	0	25	3	3	0	0	5	1	0	0	1	1	6	0	2	0	0
440-42	8	80	0	0	22	6	1	0	0	0	0	0	0	0	0	7	0	4	0	0
460-62	5	135	5	0	17	11	1	0	0	3	0	0	0	0	2	4	0	0	0	0
480-82	8	152	2	0	28	12	2	0	0	2	1	0	2	0	1	8	0	1	0	0
498-50	35	115	1	0	10	3	2	0	0	4	1	0	0	0	0	7	0	5	0	0
520-22	30	98	8	0	4	2	4	0	0	2	2	0	0	0	0	4	0	2	0	0
540-42	21	128	2	0	1	2	7	0	0	3	0	0	0	0	0	1	0	2	0	0
560-62	12	122	6	0	2	2	9	0	0	4	1	0	0	0	4	1	0	0	0	0
580-82	6	85	4	0	2	1	3	0	0	0	0	0	0	0	2	0	0	0	0	0
600-02	7	119	3	0	2	1	7	0	0	2	1	0	0	0	1	7	0	9	0	0
620-22	7	95	3	0	4	2	6	0	0	2	0	0	0	0	0	4	0	2	0	0
640-42	4	120	2	0	6	4	8	0	0	1	0	0	0	0	0	3	0	2	0	0
660-62	5	106	2	0	8	2	14	0	0	1	0	0	0	0	0	1	0	4	0	0
680-82	8	76	3	0	6	3	5	0	0	5	0	0	0	0	2	4	0	4	0	0
685-87	3	63	11	0	5	1	9	0	0	1	0	0	1	0	3	3	0	10	0	0
690-92	7	65	4	2	6	4	11	0	0	4	1	0	1	0	2	5	0	2	0	0
700-02	6	77	6	0	8	4	30	0	0	1	0	0	0	0	0	9	0	1	0	0
705-07	1	50	5	0	4	4	7	0	0	2	0	0	2	0	1	2	0	4	0	0

	PSEW	SCHF	PENN	HOHE	PLAG	MELI	METR	METL	WEIN	GRIS	LAUR	POMA	ASCA	COMP	PLAN	COPR	CRAR	DRPH	MYRS	HEBE
398-40	0	0	0	0	0	0	2	0	17	2	0	0	3	0	0	2	0	0	0	0
420-22	0	0	0	0	0	0	1	3	3	0	0	0	0	0	0	7	0	0	7	0
440-42	0	0	1	0	0	0	2	0	2	1	0	0	0	0	0	8	0	0	0	0
460-62	0	0	1	0	0	0	2	0	0	0	0	0	3	0	0	2	0	0	1	0
480-82	0	0	1	0	0	0	4	0	1	0	0	0	0	0	0	3	0	0	2	0
498-50	0	0	0	0	0	0	2	1	5	0	0	0	2	3	0	0	0	0	1	0
520-22	0	0	0	0	0	0	2	2	8	1	0	0	3	0	0	1	0	0	1	0
540-42	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	4	0	0	0	0
560-62	0	0	0	0	0	0	0	0	4	0	0	0	2	0	0	1	0	0	2	0
580-82	0	0	0	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0
600-02	0	0	0	0	0	0	3	0	10	0	0	0	2	0	0	3	0	0	0	0
620-22	0	0	0	0	0	0	4	0	9	0	0	0	1	0	0	2	0	0	1	0
640-42	0	0	0	0	0	0	1	0	8	0	0	0	0	0	0	1	0	0	0	0
660-62	0	0	0	0	0	0	4	0	9	1	0	0	0	0	0	2	0	0	0	0
680-82	0	0	0	0	0	0	1	1	27	0	0	0	0	2	0	2	0	0	2	0
685-87	0	0	0	0	0	0	3	0	34	2	0	0	1	0	0	4	0	0	0	0
690-92	0	0	0	0	0	0	3	0	24	0	0	0	0	0	0	4	0	0	2	0
700-02	0	0	0	0	0	0	2	0	44	0	0	0	2	0	0	2	0	0	0	0
705-07	0	0	0	0	0	0	5	0	48	0	0	0	0	0	0	0	0	0	2	0

	PENT	PHYL	DINL	D.BD	D.BF	CASU	LEPT	SALX	CYAT	CHEN	MUEH	RUBS	RIPO	COLS	EPIL	GRAM	ASTA	COLL	ACAE	UMBL
398-40	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0	4	1	0	0	0
420-22	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	6	0	0	0	0
440-42	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
460-62	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	5	0	0	0	0
480-82	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
498-50	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	6	0	0	0	0
520-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
540-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
560-62	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
580-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
600-02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
620-22	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
640-42	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
660-62	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
680-82	0	2	0	0	5	0	1	0	0	0	0	0	0	0	0	6	1	0	0	0
685-87	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	5	0	0	0	0
690-92	0	4	0	0	0	0	5	0	0	0	0	0	0	0	0	4	0	0	0	0
700-02	0	1	0	0	2	0	8	0	0	0	0	0	0	0	0	1	0	0	0	0
705-07	0	5	0	3	0	0	1	0	0	1	0	0	0	0	0	3	0	0	0	0

	HYDR	CRUC	TARX	RUMX	RANU	EARS	CALR	REST		TYPH	MYRI	GUNN	HALO	PHOR	CYPR				C.SM	C.DE
398-40	0	0	0	0	0	0	0	0	0	0	0	0	1	0	8	0	0	0	61	0
420-22	0	0	0	1	0	0	0	0	0	0	0	0	0	0	10	0	0	0	56	0
440-42	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	0	0	46	0
460-62	0	0	0	0	0	0	1	0	0	0	0	0	1	0	5	0	0	0	58	0
480-82	0	0	0	0	0	0	0	0	0	0	4	0	0	0	2	0	0	0	37	0
498-50	0	0	0	0	0	0	2	0	0	1	5	0	1	0	5	0	0	0	47	0
520-22	0	0	0	0	0	0	0	0	0	0	1	0	0	0	6	0	0	0	38	0
540-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	28	0
560-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	27	0
580-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	80	0
600-02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0
620-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	48	0
640-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	30	0
660-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0
680-82	0	0	0	0	1	0	0	0	0	0	0	0	0	0	6	0	0	0	26	0
685-87	0	0	0	0	1	0	0	0	0	0	0	0	0	1	6	0	0	0	14	0
690-92	0	0	0	0	0	0	0	0	0	2	0	0	0	0	6	0	0	0	23	0
700-02	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5	0	0	0	23	0
705-07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	18	0

	C.ME	D.FI	D.SQ	D.LA	PTER	LYCO	L.SC	L.LA	PHYM	POLY	PYRR	GLEI	BLCH	ASPL	HYMN	L.RA	MFER	HIST		HYPO
398-40	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
420-22	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
440-42	0	0	3	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
460-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
480-82	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
498-50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
520-22	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
540-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
560-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
580-82	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
600-02	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
620-22	0	0	3	0	0	2	0	0	1	0	0	0	0	0	0	0	1	0	0	0
640-42	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	3	0	0	0
660-62	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0
680-82	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
685-87	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
690-92	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	0	0
700-02	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
705-07	0	0	2	0	0	3	0	0	1	0	0	0	0	0	0	0	4	0	0	0

	TRIL	DRAP	DISC	UNWN																
398-40	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
420-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
440-42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
460-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
480-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
498-50	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
520-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
540-42	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
560-62	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
580-82	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
600-02	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
620-22	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
640-42	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
660-62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
680-82	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
685-87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
690-92	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
700-02	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
705-07	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX IIIa. Vegetation data and Species Lists for sampling sites, Harihari, Westland

In conjunction with the surface sampling (Chapter 5), a vegetation survey was made at each site located in the Harihari region of South Westland. This appendix tabulates the results of this survey in the form of basal areas (expressed as a per cent of the total), ground cover (density per m^2) and species lists for plants growing at and near the site of surface sample collection.

SALTWATER I

	BASAL AREA	GROUND COVER
GYMNOSPERMS		
Dacrycarpus dacrydioides	80.12	1.3
DICOTYLEDONS		
Aristotelia fruticosa		-
Cardamine uniflora		0.5
Carpodetus serratus	0.4	0.3
Clematis sp.		0.5
Coprosma ciliata		0.06
C. foetidissima	0.1	0.3
C. linearifolia		
C. rotundifolia	0.02	0.1
Griselinia littoralis	0.61	
Metrosideros perforata		4.7
Melicytus ramiflorus	0.06	-
Myrsine divaricata		
Nertera depressa		0.7
N. dichondraefolia		5
Parsonsia heterophylla		0.3
Pennantia corymbosa	0.1	0.3
Pseudopanax arboreum		0.5
P. crassifolius	1.25	0.06
P. sinclairii		-
Pseudowintera colorata		-
Schefflera digitata		-
Weinmannia racemosa	10.14	0.2
MONOCOTYLEDONS		
Astelia nervosa		0.1
Dendrobium sp.		-
Microlaena avinacea		-
Pterostylis banksii		0.3
Ripogonum scandens		0.5
Uncinia uncinata		1.0

	BASAL AREA	GROUND COVER
PTERIDOPHYTES		
Asplenium bulbiferum		3.3
A. flaccidum		0.3
Blechnum fluviatile		-
B. lanceolatum		0.2
B. procerum		-
Ctenopteris heterophylla		0.06
Cyathea smithii	3.5	0.06
Dicksonia squarrosa	3.8	0.5
Grammitis billardierii		0.06
Hymenophyllum demissum		1.0
H. dilatatum		-
Lycopodium fastigiatum		-
Phymatosorus diversifolius		0.3
Pyrrosia serpens		-
Trichomanes reniforme		0.1
T. venosum		0.1
SALTWATER II		
GYMNOSPERMS		
Dacrycarpus dacrydioides	61.7	1.2
Dacrydium colensoi		-
Podocarpus ferrugineus	9.4	-
P. spicatus	8.1	0.06
DICOTYLEDONS		
Acaena anserinifolia		0.7
Cardamine uniflora		0.06
Carpodetus serratus	3.4	0.7
Coprosma ciliata		0.06
C. rhamnoides		0.7
C. rotundifolia	0.73	0.06
Cyathodes fasciculata		0.1
Griselinia littoralis		0.2
Hedycarea arborea		
Melicytus lanceolata		0.3
M. ramiflorus		6.7
Metrosideros perforata		
Myrsine australis		1.3
Nertera dichondraefolia		0.1
Parsonsia heterophylla		1.7
Pennantia corymbosa	2.66	0.1
Pseudopanax arboreum		1.7
Pseudowintera colorata	0.44	0.06
Rubus cissoides		
R. parvus		
Schefflera digitata		
Urtica ferox		0.1
Weinmannia racemosa		
MONOCOTYLEDONS		0.7
Astelia nervosa		
Collospermum hastatum		
Cordyline australis		
Dendrobium sp.		
Microlaena avinacea		

	BASAL AREA	GROUND COVER
Pterostylis banksii		0.5
Ripogonum scandens		0.1
Uncinia uncinata		3.3
PTERIDOPHYTES		
Asplenium bulbiferum		2.5
A. falcatum		0.3
A. flaccidum		0.1
Blechnum colensoi		
B. fluviatile		
B. lanceolatum		0.1
B. procerum		
Cyathea smithii	12.5	0.3
Dicksonia squarrosa	1.1	1.5
Phymatosorus diversifolius		0.7
Polystichum richardii		
P. vestitum		
Pyrrosia serpens		
Rumohra adiantiformis		
Todea hymenophylloides		0.2
T. superba		0.06
Trichomanes venosum		4.0
FLAX ROAD		
GYMNOSPERMS		
Dacrycarpus dacrydioides		
Dacrydium colensoi		
D. cupressinum	62.5	0.36
Phyllocladus alpinus	1.9	0.16
Podocarpus ferrugineus		0.06
P. hallii	0.49	0.06
DICOTYLEDONS		
Carpodetus serratus		
Coprosma foetidissima	0.02	0.06
C. linearifolia		
C. lucida		
C. rhamnoides		0.36
Coriaria arborea		
Elaeocarpus hookerianus		0.06
Griselinia littoralis		
Hebe salicifolia		
Metrosideros perforata		0.5
M. umbellata		
Myrsine australis		
M. divaricata		0.06
Nertera dichondraefolia		0.24
Pittosporum tenuifolium		
Pseudopanax colensoi		0.06
P. crassifolius	1.36	0.2
Pseudowintera colorata		
Quintinia acutifolia	5.33	0.16
Rubus cissoides		
Weinmannia racemosa	24.81	1.12

	BASAL AREA	GROUND COVER
MONOCOTYLEDONS		
Astelia sp.		
Collospermum hastatum		
Leptocarpus simplex		
Libertia pulchella		0.06
Microlaena avinacea		
Ripogonum scandens		
PTERIDOPHYTES		
Blechnum capense		
B. discolor		
B. minus		0.16
B. procerum		
Cyathea smithii		
Dicksonia squarrosa	3.59	0.23
Gleichenia circinata		
Grammitis billardierii		
Histiopteris incisa		
Hymenophyllum demissum		
Pteridium aquilinum		
Todea superba		
Trichomanes reniforme		
SNAKE CREEK		
GYMNOSPERMS		
Dacrycarpus dacrydioides	3.5	4.1
Dacrydium colensoi	4.3	0.06
D. cupressinum	11.6	
Podocarpus ferrugineus		0.1
P. spicatus		
P. totara var. *waihoensis*	1.74	
DICOTYLEDONS		
Acaena anserinifolia		0.3
Aristotelia serrata		0.1
Carpodetus serratus	1.49	0.1
Clematis montana		0.5
Coprosma ciliata	0.15	5.0
C. foetidissima	0.22	
Coriaria arborea		
Fuchsia excorticata		
Griselinia littoralis	6.0	0.4
Hedycarea arborea		
Melicytus ramiflorus		
Metrosideros perforata		1.8
M. umbellata		
Nertera depressa		8.3
N. dichondraefolia		2.7
Paratrophis microphylla		
Pennantia corymbosa	1.12	0.2
Pseudopanax crassifolius	1.58	0.5
Pseudowintera colorata	2.45	1.3
Quintinia acutifolia		
Ranunculus hirtus		0.3
Rubus australis		
Schefflera digitata		0.4

	BASAL AREA	GROUND COVER
Urtica dioica		0.06
Weinmannia racemosa	54.51	0.4
MONOCOTYLEDONS		
Collospermum sp.		
Cordyline australis		
Corybas trilobus		1.0
Dendrobium sp.		
Freycinetia banksii		
Gramineae		6.7
Libertia pulchella		0.3
Microlaena avinacea		
Pterostylis banksii		0.3
Ripogonum scandens		
Uncinia uncinata		1.9
PTERIDOPHYTES		
Asplenium bulbiferum		0.2
A. falcatum		0.06
Blechnum colensoi		
B. discolor		
B. fluviatile		0.8
B. lanceolatum		
B. procerum		
Ctenopteris heterophylla		0.06
Cyathea smithii	6.4	0.3
Cyclosorus pennifera		
Dicksonia squarrosa	4.9	0.3
Grammitis billardierii		0.3
Hymenophyllum multifidum		0.9
Phymatosorus diversifolius		
Polystichum vestitum		0.5
Rumohra hispida		
Tmesipteris tannensis		0.2
HARIHARI		
GYMNOSPERMS		
Dacrycarpus dacrydioides		0.5
Dacrydium cupressinum	18.8	0.8
Podocarpus ferrugineus	24.8	6.5
P. hallii		
DICOTYLEDONS		
Ascarina lucida	1.2	1.8
Coprosma ciliata		0.3
C. foetidissima		0.5
C. lucida		0.3
Elaeocarpus dentatus	5.5	
Griselinia littoralis		1.1
Hedycarea arborea	0.22	0.7
Laurelia novae-zelandiae		
Metrosideros diffusa		8.0
M. perforata		4.0
M. umbellata	0.08	0.4
Nertera dichondraefolia		1.2
Pseudopanax crassifolius		

	BASAL AREA	GROUND COVER
Quintinia acutifolia	8.1	2.9
Weinmannia racemosa	41.4	0.8
MONOCOTYLEDONS		
Astelia sp.		
Earina autumnalis		0.2
Freycinetia banksii		
Libertia pulchella		0.2
Microlaena avinacea		
Ripogonum scandens		
PTERIDOPHYTES		
Asplenium flaccidum		0.4
Blechnum discolor		0.5
Cyathea smithii		
Dicksonia squarrosa		0.4
Grammitis billardierii		0.1
Hymenophyllum demissum		8.0
Phymatosorus diversifolius		0.1
Pyrrosia serpens		
Rumohra adiantiformis		
Trichomanes reniforme		
EVANS ROAD		
GYMNOSPERMS		
Dacrycarpus dacrydioides	51.7	0.8
Dacrydium colensoi		
Libocedrus bidwillii	0.10	
Podocarpus ferrugineus		0.1
P. totara var. *waihoensis*		
DICOTYLEDONS		
Acaena anserinifolia		0.5
Aristotelia serrata	1.80	0.3
Carpodetus serratus		0.06
Clematis foetida		0.3
Coprosma ciliata	0.20	0.1
C. rhamnoides		0.4
C. rotundifolia	0.52	0.3
Fuchsia excorticata		0.4
Griselinia littoralis		
Leptospermum scoparium	30.3	
Melicytis ramiflorus		
Myrsine divaricata	0.14	0.06
Nertera depressa		0.4
Parsonsia heterophylla		0.7
Pennantia corymbosa		0.3
Pittosporum colensoi	4.7	0.3
P. eugenoides		0.06
Pseudopanax arboreum	1.9	0.5
P. crassifolius	8.6	0.3
Pseudowintera colorata		
Rubus cissoides		0.5
Schefflera digitata		

	BASAL AREA	GROUND COVER
MONOCOTYLEDONS		
Agrostis tenuis		0.06
Astelia nervosa		0.3
Corybas triloba		0.06
Libertia pulchella		1.6
Pterostylis banksii		
Ripogonum scandens	0.07	0.5
Uncinia uncinata		
PTERIDOPHYTES		
Asplenium bulbiferum		0.1
Blechnum fluviatile		0.3
B. lanceolatum		0.06
B. procerum		0.2
Ctenopteris heterophylla		0.2
Cyathea smithii		0.5
Dicksonia squarrosa		
Grammitis heterophylla		
Histiopteris incisa		0.3
Hymenophyllum sp.		0.2
Pellaea rotundifolia		0.06
Polystichum vestitum		

APPENDIX IIIb. Vegetation data for Lady Lake, Westland

Drake (1977) surveyed the vegetation surrounding Lady Lake. The method employed to survey woody stemmed plants was the "Constant Count Plot" technique developed by the New Zealand Forest Service.

The data listed below is information gained from three separate vegetation survey areas. This has been grouped to give an overall basal area figure for each species which is then tabulated as a percentage of the total. These percentage figures have been used in Figure 54 for comparison with pollen percentages obtained from lake samples.

	Total Basal Area	% Basal Area
GYMNOSPERMS		
Dacrycarpus dacrydioides	12 229.67	19.14
Dacrydium colensoi	2.54	0.003
D. cupressinum	20 493.84	32.08
Phyllocladus alpinus	55.16	0.086
Podocarpus acutifolius	1.20	0.0018
P. ferrugineus	3 463.36	5.42
P. hallii	81.94	0.12
P. spicatus	36.17	0.056
DICOTYLEDONS		
Aristotelia serrata	17.37	0.027
Carpodetus serratus	1 122.16	1.756
Coprosma areolata	181.90	0.280
C. brunnea	2.16	0.003
C. colensoi	1.38	0.002
C. foetidissima	29.16	0.05
C. lucida	200.43	0.313
C. propinqua	110.19	0.17
C. rhamnoides	4.31	0.007
C. rotundifolia	46.02	0.072
C. rugosa	0.66	0.001
Elaeocarpus dentatus	2 733.58	4.279
E. hookerianus	188.22	0.295
Fuchsia excorticata	14.44	0.022
Griselinia littoralis	282.66	0.442
G. lucida	5.62	0.009
Hebe salicifolia	0.49	0.001
Leptospermum ericoides	154.80	0.24
L. scoparium	11.51	0.018
Melicytus ramiflorus	21.56	0.034
Metrosideros diffusa	71.28	0.11
M. fulgens	24.65	0.038
M. perforata	22.54	0.035
M. umbellata	34.22	0.053
Muehlenbeckia complexa	0.80	0.001

	Total Basal Area	% Basal Area
Myrsine australis	249.50	0.39
M. divaricata	12.93	0.020
M. salicina	70.48	0.11
Neomyrtus pedunculata	57.83	0.090
Paratrophis microphylla	3.58	0.006
Parsonsia heterophylla	0.70	0.001
Pittosporum colensoi	62.56	0.097
Pseudopanax colensoi	0.45	0.001
P. crassifolius	41.71	0.065
Pseudowintera colorata	65.71	0.103
Quintinia acutifolia	4 717.72	7.38
Rubus australis	1.83	0.003
R. cissoides	5.73	0.009
R. schmidelioides	1.94	0.003
Schefflera digitata	38.44	0.060
Ulex europensis	0.60	0.001
Weinmannia racemosa	13 775.68	21.56
MONOCOTYLEDONS		
Ripogonum scandens	14.67	0.023
PTERIDOPHYTES		
Cyathea smithii	1 817.02	2.844
Dicksonia squarrosa	1 268.46	1.985

APPENDIX IIIc. Vegetation data for Ajax Hill, south-east Otago

Quantitative data for the cushion bog and scrub-woodland communities are derived and tabulated from an extensive survey of Ajax Bog and its surrounds carried out by Johnson, Mark and Bayliss (1977). The parameter used is mean per cent cover of those species contributing more than 1% cover in one tier. The cushion bog and scrub-woodland data relate to the vegetation in the vicinity of surface samples AH-CB and AH-SW1, respectively.

	Tier			
CUSHION BOG	> 4m	0.6 - 4m	0.3 - 0.6m	< 0.3m
Leptospermum scoparium		10.2	11.7	0.5
Dracophyllum longifolium		3.1	9.0	0.6
Chionochloa rubra		1.1	1.5	
Dacrydium biforme		1.2		
Empodisma minus				37.3
Donatia novae-zelandiae				11.6
Cladia retipora (lichen)				10.4
C. sullivanii (lichen)				10.0
Cyathodes empetrifolia				4.7
Lycopodium ramulosum				4.0
Oreobolus strictus				3.3
Dicranoloma billardierii (moss)				2.7
Coprosma pumila				2.6
Pentachondra pumila				2.4
Riccardia cochleata (liverwort)				1.2
Celmisia gracilenta				1.2
Other species		0.4		7.5
TOTAL		16.0	22.2	100.0

SCRUB-WOODLAND	Tier > 4m	0.6 - 4m	0.3 - 0.6m	< 0.3m
Libocedrus bidwillii	5.5	3.8	0.4	0.1
Dracophyllum longifolium	0.2	31.9	1.4	0.2
Dacrydium biforme	0.3	14.6	12.3	2.4
Coprosma foetidissima		13.0	6.1	2.0
Phyllocladus alpinus		9.8	5.5	0.1
Pseudopanax simplex		5.9	0.9	0.1
Phormium cookianum		3.5	3.4	2.4
Myrsine divaricata		3.5	3.9	0.7
Coprosma astonii		2.3	8.2	1.4
Pseudopanax colensoi		2.9	5.3	2.4
Coprosma colensoi		1.5	3.0	3.8
Astelia nervosa		0.2	0.2	2.0
Cyathodes empetrifolia				5.4
Hymenophyllum multifidum				4.8
Luzuriaga parviflora				3.5
Pernettya macrostigma				3.3
Blechnum minus				2.3
Aporostylis bifolia				1.0
Cryptogams				29.5
Other species				5.2
Litter				27.4
TOTAL	6.0	93.4	50.9	100.0

APPENDIX IV

The following have been presented during the course of this work:

Relative pollen representation in relation to vegetation composition, Westland, New Zealand.

New Zealand Journal of Botany 16: 379-86 (1978).

Morphology and fine structure of conifer pollen as revealed by electron microscopy.

Ninth New Zealand Society for Electron Microscopy Conference, Christchurch 1978 *Abstracts*.

MORPHOLOGY AND FINE STRUCTURE OF CONIFER POLLEN AS REVEALED BY ELECTRON MICROSCOPY

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The morphology and fine structure of pollen representing the New Zealand conifer genera Podocarpus and Dacrydium is investigated using scanning and transmission electron microscopy. Form and surface characteristics are clearly revealed under the scanning electron microscope. Morphological variations between species are shown which are of considerable comparative and diagnostic importance.

Transmission electron microscope studies confirm the following:

(1) the sacci peculiar to conifer pollen grains are formed by a distension of the outer layer of the pollen wall;
(2) the sporopollenious exine is two layered consisting of an inner laminated layer (the nexine) and an outer one (the sexine) which is a sculptured granular layer;
(3) variations in the thickness of the sexine are shown to delineate the cap and furrow regions of the grain.

New Zealand Journal of Botany, 1978, Vol. 16: 379-86.

Relative pollen representation in relation to vegetation composition, Westland, New Zealand

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(Received 14 October 1977)

ABSTRACT

Moss cushions were collected at six localities near Harihari, South Westland, and analysed for their pollen content. Basal area data were compiled for all plants over 1.5 m tall at each locality. Comparison of vegetation and pollen data indicates that *Coprosma, Phyllocladus,* and *Cyathea* are over-represented; *Dacrydium cupressinum, Quintinia, Pennantia,* and *Dicksonia* are more-or-less proportionately represented; and *Weinmannia, Dacrycarpus, Metrosideros, Podocarpus ferrugineus, P. spicatus,* and *Dacrydium colensoi* are under-represented. Limited application was found for R-values in this study.

INTRODUCTION

The application of modern pollen rain data to fossil pollen assemblages provides a first approximation in the interpretation of vegetation history (McAndrews & Wright 1969). This has been accepted as a primary basis for the interpretation of fossil pollen assemblages even though some vegetation types may be no longer extant, some species have become extinct or have formed new vegetation types.

To date, modern pollen rain studies in New Zealand have involved the use of pollen traps in urban areas (Clark 1951, Licitis 1953) or considered surface samples within vegetation areas (Moar 1969, 1970, 1971; McKellar 1973; Myers 1973; Dodson 1976). These provided a qualitative description of the vegetation surrounding the sampling sites to relate modern pollen rain to the vegetation. The aim of this paper is to relate pollen rain analysed from surface samples to a quantitative description of some vegetation types in the Harihari region of South Westland.

Davis (1963) developed a method which uses species abundance and pollen frequency data to calculate the "R-value", the ratio between the percentage of a given taxon in the pollen rain to its percentage in the vegetation:

$$R(a) = \frac{\text{species "a" pollen percentage}}{\text{species "a" vegetational percentage}}$$

The terms "over-representation" or "under-representation" depend on whether the R-value is larger or smaller than 1 (Flenley 1973, Dodson 1975). However, the R-value for a species may vary from site to site, especially in regions where the relative importance of heavy to light pollen-producing species differs (Livingstone 1968, Oldfield 1970). The R-values for some species are considered in this paper to establish their value in New Zealand pollen studies.

VEGETATION OF THE HARIHARI AREA

Before clearance the seaward morainic slopes and terraces in the Harihari region of South Westland supported a mosaic of podocarp–hardwood forests (Godley 1976). *Dacrydium cupressinum* dominates except in isolated areas of special character such as wet swampy localities where *Dacrycarpus dacrydioides* prevails, natural basins at low altitudes where *Dacrydium colensoi* forms bog forests, and areas of recent alluvium where *Podocarpus spicatus* and *P. totara* var. *waihoensis* dominate (Holloway 1954). *P. ferrugineus* is commonly associated with *Dacrydium cupressinum* and on steeper slopes (e.g., Poerua State Forest behind Harihari settlement) may attain similar densities. *Weinmannia racemosa* and *Quintinia acutifolia* form an important component of these vegetation complexes and in some instances may be numerically dominant. Most of the cleared land (i.e., river flats) is used for dairying. In addition, the understorey of some forests shows evidence of grazing by cattle and past logging activities by the New Zealand Forest Service.

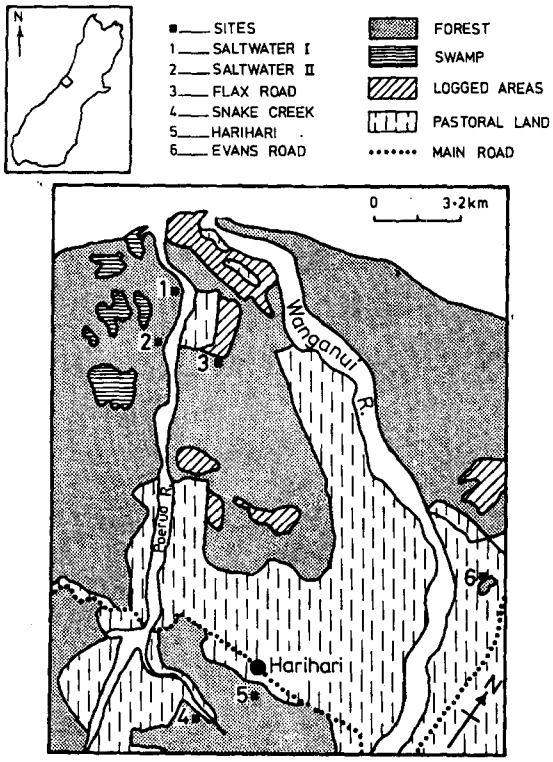

Fig. 1 Location of sites in the Harihari region, South Westland.

METHODS

Vegetation

Sampling sites were chosen to represent a range of vegetation types and were located with the aid of maps compiled during the National Forest Survey of 1955. Species abundance in the vegetation was determined in the summer of 1976–77. A quantitative study was made of the vegetation at each site: a transect 5 m wide by 30 m long was marked off and all stems > 1 cm girth breast height (at 1.5 m above ground surface) were identified and their circumferences measured. A minimum of 100 individuals was counted, which often meant that the sample area had to be extended. The data were later converted to basal area and are summarised in Table 1. This measure takes account of the higher pollen production of larger trees (Davis & Goodlett 1960) and despite difficulties in its use permits speculation on the relationships between vegetation and pollen rain (Whitehead & Tan 1969).

Pollen rain

Moss and liverwort cushions of similar thickness and texture were used to determine the pollen rain at each site. To minimise the possibility of differential filtration of pollen and spore types by the cushion its whole thickness was removed (Dodson 1976). An attempt was made to collect all moss cushions in openings in the forest, thus avoiding overrepresentation of canopy species, but this was not always possible and some samples were collected under the canopy and consequently near source trees. At each site (Fig. 1) six moss cushions were collected at random from the transect. In the laboratory the samples (in sub-samples) were boiled in 5% sodium hydroxide solution, sieved through a 100–μm mesh to remove most of the material, and acetolysed (Erdtman 1960). If silica was present hydrofluoric acid was used after the alkali treatment. Dehydration through an ethanol series followed and the residue was mounted in silicone oil (2 000 cSt) on a microscope slide.

Pollen and spore counts were carried out at a magnification of ×400 and no less than 300 pollen grains were counted per sample along successive traverses of the slides. The pollen sum (on which percentage calculations are based) includes all pollen and spores counted. The percentages in Table 2 are the means of all samples at each site. Fig. 2 compares the basal area data and pollen frequencies for the major tree types.

VEGETATION AND POLLEN RAIN AT EACH SAMPLING SITE

In the following the values in parentheses represent percentages of total basal area of plants > 1.5 m tall and those in square brackets the percentage of total pollen and spores. Comparative data relating pollen frequency to basal area for tree types are summarised in Table 1 and Fig. 2. R-values have been calculated for each taxon; these are also indicated in Table 1.

Saltwater I (NZMS 1 S63:043134, Fig. 1)

The forest at this site is an almost pure stand of *Dacrycarpus dacrydioides* (80) in a swampy locality on the southern bank of the Poerua River. It is one of the few remnants of its type left in Westland. Under the dense *Dacrycarpus* canopy exist scattered individuals of *Weinmannia racemosa* (10), *Carpodetus serratus* (1), *Pseudopanax crassifolius* (1), *Dicksonia squarrosa* (4), and *Cyathea smithii* (3.5).

Table 1 Total basal area, pollen representation, and R-values for tree types, Harihari, South Westland.
(Pollen sum = total pollen + spores)

	Saltwater I			Saltwater II			Flax Road			Snake Creek			Harihari			Evans Road		
	Basal area %	Pollen %	R-value	Basal area %	Pollen %	R-value	Basal area %	Pollen %	R-value	Basal area %	Pollen %	R-value	Basal area %	Pollen %	R-value	Basal area %	Pollen %	R-value
Dacrycarpus dacrydioides	80.12	38.4	0.5	61.7	6.4	0.1	—	2.7	—	3.5	2.7	0.8	—	0.3	—	51.7	14.4	0.3
Dacrydium cupressinum	—	2.4	—	—	0.9	—	62.5	42.2	0.7	11.6	22.1	1.9	18.8	13.2	0.7	—	2.4	—
D. colensoi	—	0.6	—	—	0.5	—	—	2.1	—	4.3	0.1	0.02	—	0.1	—	—	1.3	—
Phyllocladus alpinus	—	0.4	—	—	0.6	—	1.9	5.7	3.0	—	0.7	—	—	0.7	—	—	0.4	—
Podocarpus ferrugineus	—	1.8	—	9.4	0.3	0.03	—	3.4	—	—	1.8	—	24.8	13.7	0.6	—	1.4	—
P. spicatus	—	—	—	8.1	1.3	0.2	—	0.1	—	—	0.4	—	—	0.8	—	—	—	—
Ascarina lucida	—	0.1	—	—	—	—	—	0.6	—	—	0.4	—	1.2	3.8	3.2	—	0.3	—
Carpodetus serratus	0.4	0.2	0.5	3.4	0.09	0.03	—	0.03	—	1.5	0.1	0.07	—	0.3	—	—	0.1	—
Coprosma	0.1	5.2	52.0	0.7	1.7	2.4	0.02	4.2	210	0.4	3.0	7.5	—	1.3	—	0.7	4.9	7.0
Elaeocarpus	—	0.4	—	—	1.0	—	—	1.1	—	—	0.7	—	5.5	0.1	0.02	—	6.2	—
Griselinia littoralis	0.6	1.2	2.0	—	0.6	—	—	0.5	—	6.0	2.2	0.4	—	0.7	—	—	0.6	—
Leptospermum scoparium	—	0.9	—	—	—	—	—	0.2	—	—	0.1	—	—	0.1	—	30.3	22.9	0.8
Pennantia corymbosa	0.1	0.1	1.0	2.7	14.7	5.4	—	—	—	1.1	1.0	0.9	—	0.1	—	—	1.3	—
Pseudopanax	1.3	0.8	0.6	—	0.7	—	1.4	0.3	0.2	1.6	0.5	0.3	—	0.4	—	10.5	1.7	0.2
Quintinia acutifolia	—	1.2	—	—	3.1	—	5.3	2.8	0.5	—	1.4	—	8.1	9.2	1.1	—	1.0	—
Weinmannia racemosa	10.1	5.6	0.5	—	3.8	—	24.8	7.3	0.3	54.5	23.2	0.4	41.4	5.3	0.1	—	4.7	—
Cyathea smithii	3.5	2.1	0.6	12.5	36.9	3.0	—	3.8	—	6.4	17.2	2.7	—	13.7	—	—	0.9	—
Dicksonia squarrosa	3.8	5.5	1.4	1.1	1.7	1.5	3.6	0.7	0.2	4.9	3.4	0.7	—	1.8	—	—	0.2	—

Table 2 Modern pollen rain (including fern spores) percentages from surface samples, Harihari, South Westland.

(Pollen sum = total pollen + spores)

	Saltwater I	Saltwater II	Flax Road	Snake Creek	Harihari	Evans Road
Dacrydium cupressinum	2.4	0.9	42.2	22.1	13.2	2.4
D. colensoi	0.6	0.5	2.1	0.1	0.1	1.3
Dacrycarpus dacrydioides	38.4	6.4	2.7	2.7	0.3	14.4
Libocedrus	0.2	—	—	—	—	0.3
Podocarpus ferrugineus	1.8	0.3	3.4	1.8	13.7	1.4
P. spicatus	—	1.3	0.1	0.4	0.8	—
P. totara var. *waihoensis*	0.3	0.1	0.4	1.0	0.3	6.5
P. hallii	—	—	0.5	—	4.5	—
Pinus	—	0.1	0.3	—	—	—
Phyllocladus	0.4	0.6	5.7	0.7	0.7	0.4
Aristotelia	4.3	0.2	0.6	0.5	0.1	0.4
Ascarina	0.1	—	0.6	0.4	3.8	0.3
Astelia	1.9	0.4	0.3	—	0.1	0.1
Calorophus	—	0.2	0.2	0.1	—	—
Carpodetus	0.2	0.09	0.03	0.1	0.3	0.1
Collospermum	0.1	0.2	0.2	0.1	0.1	0.3
Compositae	0.8	—	0.7	—	0.1	0.2
Coprosma	5.2	1.7	4.2	3.0	1.3	4.9
Coriaria	—	0.1	0.2	0.1	—	—
Cyperaceae	0.2	0.2	1.7	0.1	0.1	1.2
Elaeocarpus	0.4	1.0	1.1	0.7	0.1	6.2
Gramineae	5.4	1.9	5.7	3.4	3.7	13.6
Griselinia	1.2	0.6	0.5	2.2	0.7	0.6
Haloragis	—	0.2	—	—	—	0.1
Leptospermum	0.9	—	0.2	0.1	0.1	22.9
Metrosideros	4.4	1.3	3.4	3.5	13.3	0.4
Myriophyllum	0.2	—	—	—	—	0.1
Myrsine	1.0	0.3	1.9	0.2	0.3	0.8
Nothofagus fusca type	0.4	0.1	0.8	0.4	0.5	0.5
N. menziesii	—	—	—	—	0.1	—
Pennantia	0.1	14.7	—	1.0	0.1	1.3
Pittosporum	—	0.1	—	—	—	0.2
Plantago	0.2	0.1	0.1	—	—	—
Pseudopanax	0.8	0.7	0.3	0.5	0.4	1.7
Pseudowintera	—	0.1	—	0.3	—	—
Quintinia	1.2	3.1	2.8	1.4	9.2	1.0
Ripogonum	—	1.5	—	—	4.4	—
Rubus	—	0.2	—	—	0.1	2.0
Rumex	—	—	—	—	0.2	—
Schefflera	—	0.3	—	—	0.1	—
Taraxacum	0.3	0.1	—	—	0.1	0.7
Typha	—	0.1	—	—	—	—
Weinmannia	5.6	3.8	7.3	23.2	5.3	4.7
Fern spores						
Asplenium	1.5	0.8	1.0	0.5	—	0.1
Blechnum	—	0.2	0.1	0.8	0.7	—
Cyathea smithii	2.1	36.9	3.8	17.2	13.7	0.9
C. dealbata	0.5	—	—	—	—	0.3
Dicksonia squarrosa	5.5	1.7	0.7	3.4	1.8	0.2
Gleichenia	—	—	—	—	—	0.2
Hymenophyllum	1.4	0.6	2.0	0.5	1.7	4.5
Lycopodium	0.1	0.4	0.4	0.4	1.0	0.2
Monolete spores	3.6	2.5	0.5	0.6	3.4	0.2
Phymatosorus	7.4	5.3	1.3	7.0	0.7	0.9
Pyrrosia	—	—	—	—	0.1	—
Unknown	—	—	—	—	0.1	2.1

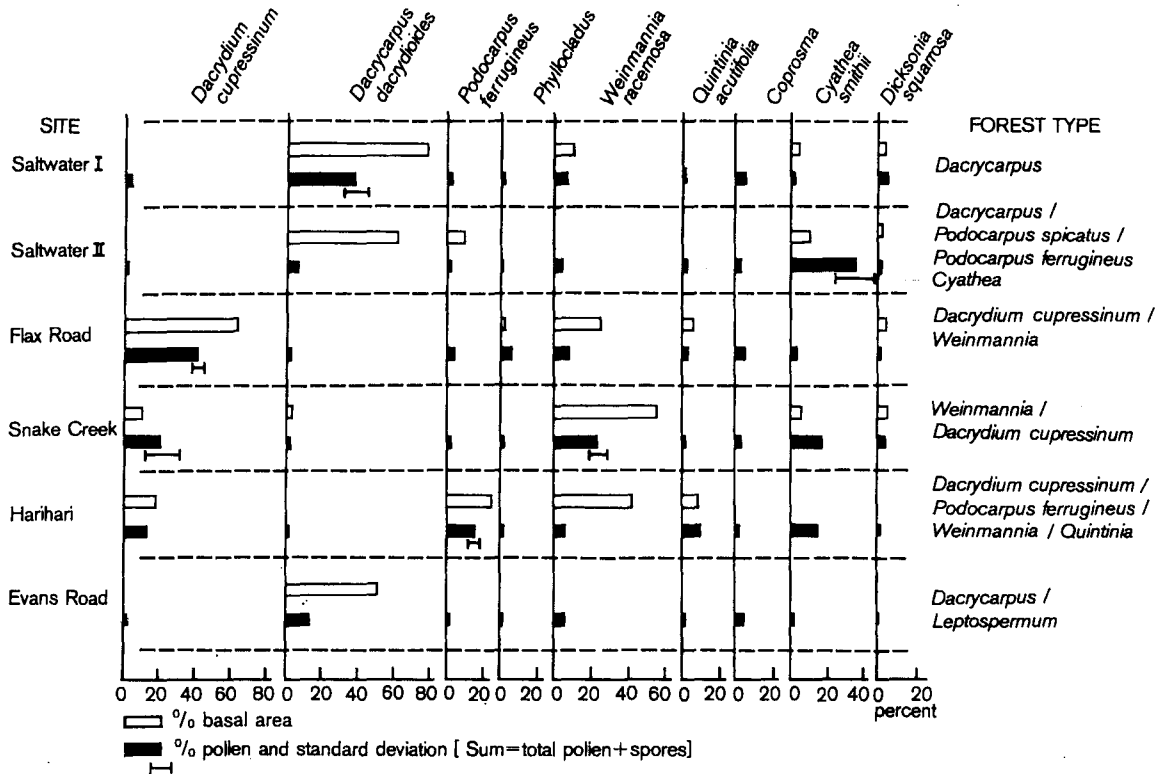

Fig. 2 Relationship between pollen rain and forest composition for main tree types, Harihari, South Westland.

There is a dense ground cover of *Metrosideros perforata, Nertera dichondraefolia, Asplenium bulbiferum,* and *Hymenophyllum* spp.

Dacrycarpus [38] is under-represented even though it dominates the pollen spectrum. This is best explained by the presence at the sampling site of *Coprosma, Weinmannia,* and *Dicksonia squarrosa.* These plants contribute, in this case, little to the basal area but shed pollen or spores close to the source trees. It is difficult to assess the representation of *Phymatosorus* spores because two of the six samples were collected near *Phymatosorus* plants.

Saltwater II (NZMS 1 S63:053110, Fig. 1)

The canopy is dominated by *Dacrycarpus dacrydioides* (62) but scattered individuals of *Podocarpus ferrugineus* (9) and *P. spicatus* (8) are present probably as a result of better soil fertility and drainage. The canopy is more open than at Saltwater I and below there is a sparse understorey consisting mainly of *Pennantia corymbosa* (2), *Carpodetus serratus* (3), *Pseudowintera colorata* (1), *Coprosma rotundifolia* (1), and *Cyathea smithii* (12.5). *Uncinia* spp. and *Metrosideros perforata* form most of the sparse ground cover.

An exceedingly low pollen frequency for *Dacrycarpus* [6] provides a striking example of the under-representation of this species. The presence of *Cyathea smithii,* a tree fern regularly over-represented in the pollen spectra, and *Pennantia corymbosa* at the site of deposition tend to conceal the *Dacrycarpus* pollen recorded in the samples. *Coprosma, Griselinia,* and *Dicksonia squarrosa* are more-or-less proportionately represented whereas *Podocarpus ferrugineus, P. spicatus,* and *Carpodetus serratus* are under-represented. A surprising feature of the pollen spectra is the low frequency of *Dacrydium cupressinum* [1], not present in the immediate sample area but forming extensive pole stands 100 m to the south. Pollen of *Quintinia* [4] is derived from a distant source.

Flax Road (NZMS 1 S63:075114, Fig. 1)

Milling operations in the 1940s (P. Mawson, pers. comm.) removed all of the *Podocarpus ferrugineus* and many of the larger *Dacrydium cupressinum* trees from the Flax Road site, however, *D.*

cupressinum remains dominant in terms of basal area (63). As a consequence of the logging, *Phyllocladus alpinus* (2), *Weinmannia racemosa* (25), and *Quintinia acutifolia* (5) have become abundant in the understorey. The ground cover is limited mainly to *Sphagnum* moss due to poor drainage and past disturbances.

Dacrydium cupressinum [42] is well represented and dominates the pollen spectrum. Irregularity of *D. cupressinum* flowering in the years since logging and the presence of the locally over-represented genera *Coprosma, Phyllocladus,* and *Cyathea* may account for the disparity between the basal area and the pollen percentages. The pollen frequency for *Podocarpus ferrugineus* [4] probably results from its occurrence before logging.

Snake Creek (NZMS 1 S64:138973, Fig. 1)

This site is in a stand of *Weinmannia racemosa* (55) with scattered podocarps of which *Dacrydium cupressinum* (12), *D. colensoi* (4), and *Dacrycarpus dacrydioides* (3.5) are the most important. The understorey is dominated by *Cyathea smithii* (6), *Dicksonia squarrosa* (5), *Pseudowintera colorata* (2.5), *Carpodetus serratus* (1.5), *Pennantia corymbosa* (1), and *Coprosma* spp. (0.5). A feature of the ground cover is the dense mat formed by *Nertera depressa, N. dichondraefolia, Metrosideros perforata,* and numerous ferns. The forest at this site is degraded in places because of grazing animals and aggradation resulting from recent erosion of the hills above.

Weinmannia [23] and *Dacrydium cupressinum* [21] are equally well represented in the pollen spectra despite the much greater basal area of *Weinmannia.* Much of the *D. cupressinum* pollen falls close to the source trees, leading to local over-representation. *Coprosma, Phymatosorus,* and *Cyathea* are over-represented; *Dicksonia, Metrosideros,* and *Pseudopanax* proportionately represented; and *Dacrycarpus, Dacrydium colensoi, Pseudowintera,* and *Carpodetus* under-represented. Despite the dense herbaceous ground cover very little herb pollen was recorded.

Harihari (NZMS 1 S64:160022, Fig. 1)

This site lies on a moderately steep slope behind the Harihari settlement. The canopy is dominated by *Podocarpus ferrugineus* (25), *Dacrydium cupressinum* (18), *Weinmannia racemosa* (41), *Quintinia acutifolia* (8), and *Elaeocarpus dentatus* (5). *P. ferrugineus* had more individuals but *D. cupressinum* trees are larger boled. The understorey is sparse with *Ascarina lucida* (1), *Hedycarya arborea* (1), and *Metrosideros umbellata* (1) as its major components. The ground cover has been browsed by goats, but their recent extermination from the area has seen an upsurge in podocarp–hardwood regeneration accompanied by *Hymenophyllum* spp. and the slender lianes *Metrosideros perforata* and *M. diffusa.*

Pollen of *Podocarpus ferrugineus* [14], *Dacrydium cupressinum* [13], and *Metrosideros* [13] dominate the pollen spectrum. *P. ferrugineus* is slightly under-represented. The pollen of *Metrosideros* is derived from three species, making the role of this genus in the pollen rain difficult to assess. *Podocarpus hallii, Ascarina,* and *Ripogonum* when near the sampling site are proportionately represented. *Quintinia* is proportionately represented but *Weinmannia* and *Elaeocarpus* are substantially under-represented. *Cyathea* spores are derived by upward drift from gullies at lower altitudes where *Cyathea* is prominent.

Evans Road (NZMS 1 S64:214102, Fig. 1)

Evans Road Bush is an association of shrubs and small trees. Covering *c.* 21 ha and surrounded by pasture it is a last remnant of bush cover which once occupied large areas of the Wanganui River flood plain. *Dacrycarpus dacrydioides* (52) is dominant, accounting for 38 of the 100 trees and saplings measured in the survey. *Leptospermum scoparium* (30), *Pseudopanax* spp. (10), and *Pittosporum colensoi* (5) combine with *Dacrycarpus* to form an almost closed continuous canopy. *Podocarpus totara* var. *waihoensis* and *Dacrydium colensoi* are present around the fringes of the sampling area but are not included in the vegetation analysis. The understorey has been considerably disturbed by domestic animals and consists of ferns, *Libertia pulchella,* and grasses.

Although *Dacrycarpus dacrydioides* is the commonest tree species the pollen spectrum is dominated by *Leptospermum* [23]. The presence of many immature individuals not yet contributing to the pollen rain may explain the under-representation of *Dacrycarpus.* Of the other taxa *Coprosma* is over-represented, *Leptospermum* is proportionately represented, and *Pseudopanax* and *Pittosporum* under-represented. *Elaeocarpus pollen* [6] may have come from trees that have since disappeared from the bush. A feature of the pollen spectrum is the deposition of pollen from outside the immediate area — mainly Gramineae [13] and *Podocarpus totara* var. *waihoensis* [6.5]. *Weinmannia, Dacrydium cupressinum, Podocarpus ferrugineus, Cyathea,* and *Quintinia* are derived from more-distant sources.

DISCUSSION

Dacrydium cupressinum is more-or-less proportionately represented in the pollen spectra, but there are exceptions. There was over-representation in some samples at Snake Creek and Harihari because the

density of the trees and an almost closed canopy restricts air circulation. The relatively low frequencies of *D. cupressinum* pollen at three sites (Saltwater I and II, Evans Road), especially in a region where it is the dominant species, appear at first to contradict earlier work. Moar (1970) reported the transport of *D. cupressinum* pollen from Westland to Canterbury and Mildenhall (1976) has noted *D. cupressinum* pollen on Chatham Island, derived from mainland New Zealand, 725 km to the west. Therefore, although *D. cupressinum* has widely dispersed pollen local representation is strongly affected by vegetation structure and dispersal of pollen of other taxa in the vegetation. The percentages of *Dacrycarpus dacrydioides* pollen are all lower than the percent basal area. This under-representation, also reported by Harris & Filmer (1947), may result from low pollen production. At Saltwater II and Harihari *Podocarpus ferrugineus* is under-represented. The low frequencies recorded at the other sites illustrate the regional presence of the species but indicate little of its importance in the vegetation. According to Moar (1970) *Phyllocladus* is over-represented when present at the sampling site. This view is supported by the Flax Road data. Relatively low pollen frequencies at the remaining sites reflect the scattered and limited distribution of *Phyllocladus* in the study area.

Weinmannia racemosa flowers profusely and is insect pollinated (Wardle 1966). Moar (1970) considers this pollen to be under-represented, an observation supported by results obtained in the present study. *Quintinia acutifolia*, the second-most important hardwood in the regional vegetation, is proportionately represented in the pollen spectra. Moar (1970) noted *Quintinia* pollen in surface samples on the Fox Range, Westland, apparently derived from lower altitudes. *Quintinia* may rely on both insects and wind for pollen dissemination. *Coprosma* was over-represented at all sampling sites. This is not surprising because *Coprosma* is anemophilous but at least part of the over-representation can be due to the tendency of basal area measures to under-represent small stemmed trees or shrubs (Whitehead & Tan 1969). *Coprosma* pollen cannot be identified to species level and it is therefore difficult to assess its role in the pollen rain.

Cyathea smithii is consistently over-represented. At Saltwater II there is extreme variation between samples, suggesting abundant spore production and relatively poor dispersal. Dodson (1976) noted a similar phenomenon with *C. dealbata*. *Dicksonia squarrosa* has a low basal area at most sites and is proportionately represented.

Pollen percentages of *Pennantia corymbosa* and *Ascarina lucida* slightly exceed the percent basal area recorded and the pollen percentages of *Leptospermum* and *Griselinia* are equal to or slightly less than their percent basal area. Within the limits of the accuracy of this study, all these genera have similar pollen representation. The pollen percentages of *Dacrydium colensoi* at Snake Creek and *Podocarpus spicatus* at Saltwater II do not reflect their importance at these localities. *Pseudopanax, Elaeocarpus, Pittosporum, Myrsine, Carpodetus serratus,* and *Pseudowintera* are under-represented, but this may be expected because they are all entomophilous. *Metrosideros* was recorded consistently, with most of the pollen contributed by the slender lianes *M. perforata* and *M. diffusa*. Wardle (1971) reports that some pollen from *M. umbellata* becomes airborne but most falls close to the source trees; the pollen frequency [13%] at Harihari, where this species was present, is probably a direct result of this.

Very low frequencies [1%] of *Nothofagus fusca* type pollen are recorded at all sampling sites. *Nothofagus* forest is absent from the area, so pollen has probably been derived from forest east of the Main Divide (Moar 1973).

At most sites *Nertera* provided a patchy but dense ground cover, however, pollen of this genus is absent from the surface spectra. Pollen of the anemophilous families Cyperaceae and Gramineae is consistently recorded, seemingly originating from the non-forested pasture regions of the river-flats between the Wanganui and Poerua Rivers. Spores of most ferns are detected in low frequencies but local over-representation of *Hymenophyllum* and *Phymatosorus* was noted.

There are serious drawbacks in the use of R-values (Table 1). Extreme variation in the values obtained from some species (e.g., *Coprosma, Griselinia, Pennantia*) may result from limitations of a vegetation survey which does not adequately account for shrub species. Accurate vegetational data must be available for a very large area to prevent irregularities in the R-values (Livingstone 1968), and also the use of R-values ignores the differential effect of varying distances on pollen dispersal (Oldfield 1970). The R-values do serve to illustrate local over-representation of some species, e.g., *Dacrydium cupressinum* at Snake Creek, *Pennantia corymbosa* at Saltwater II, *Ascarina lucida* at Harihari, and *Phyllocladus* at Flax Road, nevertheless I suggest that only limited use can be made of R-values in Westland.

Wind-pollinated taxa are proportionately represented or over-represented when compared to insect-pollinated taxa. There are, however, some exceptions, the most notable of which are the conifers *Podocarpus ferrugineus, P. spicatus, Dacrydium colensoi,* and *Dacrycarpus dacrydioides*. Although they are wind pollinated, low frequencies of these species do not imply rarity in the vegetation and high frequencies suggest their presence at the site of deposi-

tion. *Weinmannia, Metrosideros,* and *Elaeocarpus* are insect pollinated and are under-represented outside the vegetation in which they occur. Low pollen frequencies of these genera cannot be taken to indicate their absence from the sampled area. Dispersal of *Dacrydium cupressinum, Leptospermum, Phyllocladus, Coprosma,* and *Cyathea smithii* away from the forest in which they occur is surprisingly restricted. Despite large areas of pasture and swamp land in the surrounding area (Fig. 1) only small amounts of Gramineae and Cyperaceae pollen are recorded; which suggests that there is only limited pollen transport into and through forested areas. Because the samples were taken in small openings or under the canopy the local vegetation probably inhibits rain-out of pollen from the regional vegetation.

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